THE UNIVERSITY *of* EDINBURGH

THE WINTERING ECOLOGY OF OSPREYS IN SENEGAMBIA

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Jar khol, bajo, molum gueej

du napp, du nexan

te jen wu duuf rekk lay lekk

mol ag galaam

jar khol ag katanaam

kaya du am

Osprey, the special one, fisherman of the sea

he does not have nets, he does not beg for fish

and he only eats fat fish

the fisherman and his boat

the Osprey and its skills

there will not be a lack of fish

(wolof saying)

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During my first trip to Senegambia in 1977-78, it became apparent that collection of sufficient data would be impossible without field assistance. I therefore organized a University expedition and arranged for two zoology graduates to accompany me. Although the planning and direction of field work was entirely mine, Ian Patterson and, especially, Jock Baker collected substantial amounts of data on distribution and food as follows: Ian Patterson in the Saloum River delta in February 1979 and at the mouth of the Senegal River in April 1979. Jock Baker at the mouth of the Senegal River in February-March, July, September-October and December 1979; in the Saloum River delta in April-May, August and November 1979; at the Djas pond in August, October and December 1979; along the coast between the mouth of the Senegal River and the Cap-Vert peninsula in August-September and November 1979. Mr. Baker also helped me develop a trap for Ospreys and was responsible for one-third of captured Ospreys.

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ABSTRACT

Various aspects of Osprey biology, Pandion h. haliaetus, were studied from museum specimens and in the field.

Size, breast markings and crown markings were found insufficient to discriminate populations, but underwing coverts were sufficient. Four subspecies were recognized, corresponding to the Palearctic, North America, the Bahamas and Australasia. However Ospreys can be divided into two groups, a Holarctic group, consisting of Palearctic, North American and Bahaman Ospreys, and the Australasian Ospreys.

Ecology was studied in Senegambia during two visits in 1977-80. Over 800 Ospreys were estimated to winter there, mostly at river mouths and in mangrove. Marked Ospreys returned to the same area in consecutive years, and stayed within that area during winter. Dispersion along the coast was random except at a few localities where the birds concentrated. In mangrove, birds were regularly spaced at high tide but went to the coast or more open mangrove at low tide. Along the coast, Fish Eagles, Haliaeetus vocifer, and Ospreys seemed independently distributed, but in mangrove Ospreys avoided hunting in sight of a Fish Eagle, while along rivers and lakes eagles might have excluded Ospreys.

The diet consisted mostly of Mugilidae, various Clupeidae, and, during part of winter, of Exocoetidae. Average fish size was generally 200-300 g, but fish were smaller in areas well protected from the open sea. Dive success and search time per capture varied between sites, partly because they were significantly correlated with fish size. Immatures 6 months old were less succcessful at catching fish than older birds. Foraging efficiency varied from 2.9 to 10 kcal/minute of foraging. Most Ospreys were found in mangrove even though foraging efficiency was lower there. This was most likely because hunting from a perch in mangrove was less demanding than hunting from flight elsewhere.

Moult was studied from captured Ospreys and museum skins. A few Ospreys were caught more than once so that the development of the moult pattern of the primaries could be traced. Limits to the growth rate of feathers are emphasized as a major reason for the evolution of the Staffelmauser pattern of moult in large birds.

Ospreys do not breed in the tropics, except in Australasia, even though the habitat seemed ecologically suited. In particular, foraging efficiency was as high in Senegambia as on the north-temperate breeding grounds. It is suggested that migrants Ospreys are physiologically inhibited from breeding in the tropics because daylength is too short, while south of the tropic of Capricorn, where migrants might be stimulated to breed, but six months out of phase, they are too scarce to start a permanent breeding population. It is suggested that non-migratory Ospreys have not spread their range south because of the presence of large numbers of migrants in the tropics.

INTRODUCTION

"In Africa we at once run up against a curious feature in the Osprey. One would think that all that would be necessary to attract a permanent resident pair of Ospreys would be a good supply of fish and a tall tree or an offshore rock or sandbank to breed on. This is what seems to be necessary to Europe, North America and Australia. But the fact is that south of Somalia and Morocco (excepting for the Atlantic Islands) Ospreys are either absent as breeding birds or extremely rare. They do not seem to take advantage of the abundant food supply and suitable tall trees that occur in and around many African lakes or coastal lagoons. Thus here again, as in harriers and some kestrels, there is an apparently available ecological niche which is not filled..... All we can say is that it is inexplicable." (Brown, 1970, pages 134-135).

The absence of breeding Ospreys, Pandion haliaetus, in Africa is made the more curious by the presence of wintering migrants from Europe. An analogous situation exists in the Americas and in Asia, with migrants from North America and northern Asia wintering in South America and southern Asia respectively, but no Ospreys breeding there.

Although Ospreys have been extensively studied on their breeding grounds of Europe and North America, they have never been studied on their tropical wintering grounds. This thesis attempts to fill this gap and at the same time addresses itself to the more general problem mentionned above.

Field work was done in Senegambia in November 1977-April 1978 and December 1978-June 1980. The results are discussed in Chapters 2 and 3. Much attention was given to ecological factors, in particular the availability of food, that might keep Ospreys from breeding in Senegambia. This data is used in Chapter 5 to discuss why Ospreys do not breed in the tropics.

Wing moult was first studied with the intention of using moult patterns to age Ospreys. However, I gradually became interested in the pattern of moult itself and its evolutionnary causes. These matters are discussed in Chapter 4.

Museum specimens were first studied to determine whether differences in morphology between populations would reveal past patterns of dispersal. It was necessary to verify the validity of subspecies, especially since there was no subspecific distinction between resident and migratory populations. The result of this work is discussed in Chapter 1.

Since it was not relevant to the theme of the thesis, I have placed in an appendix a description of a trap which Jock Baker and myself developed for catching Ospreys. I have included as a second appendix part of the data on diet discussed in Chapter 3.

CHAPTER 1

OSPREY DISTRIBUTION AND SUBSPECIES TAXONOMY

1.1 INTRODUCTION

Palearctic and American Ospreys were first placed in the same genus by Vieillot (1822), to which genus Gould (1837) later added a third species, the Australasian Osprey. This classification was still accepted in 1877 by Giebel, although by then Schlegel (1862) had suggested lumping all Ospreys into one species. This was explicitly done by Baird et al. (1874), for the Palearctic haliaetus and the North American carolinensis. Sharpe (1874) went further and lumped these two forms into one subspecies, though he kept Australasian Ospreys as a separate species. The classification with two species and three subspecies held until Maynard (1887) added a third species, the Bahaman Osprey, previously lumped with North American Ospreys. Riley (1905) reduced this to the subspecies, ridgwayi, and by then Knowlton and Ridgway (1909) had recognized Schlegel's (1862) opinion and reduced the Australasian Osprey to the subspecies leucocephalus (corrected to cristatus by Hartert, 1921). The Osprey thus became one species with four subspecies, although Hartert (1921, 1923) never accepted the splitting of American

Ospreys into two subspecies.

Then started a period of quibbling on subspecies, most of it on little evidence. Swann (1922) split Australasian Ospreys into two subspecies according to size: the smaller microhaliaetus in the Celebes and New Caledonia, and cristatus elsewhere. Although explicitly refuted by Hartert (1923), the split was maintained by Maxwell (1927) and Peters (1931). Later Vaurie (1965), based on work by Amadon (pers. comm.), also recognized two subspecies according to size but shifted south the limit of microhaliaetus, renaming it melvillensis. The split is still not widely accepted (Slater, 1971; Macdonald, 1973; Schodde, pers. comm.).

Wolfe (1946) added a subspecies, friedmanni, to Palearctic Ospreys based on plumage differences, while Kipp (1951) added another, mutuus, based on size differences. There is no published rebuttal of these opinions, although Vaurie (1965) implicitly considered the two new subspecies as synonyms of haliaetus. Vaurie (1965) was the last authority to comment on Osprey subspecies; Brown and Amadon (1968) simply repeat him.

Since Baird et al. (1874) lumped Palearctic and North American Ospreys, there has been no meticulous comparison of Osprey subspecies. In particular:

- The opinions of Wolfe and Kipp have not been properly refuted.
- The opinions of Swann, Maxwell, Peters, Vaurie and Brown and

Amadon on the splitting of cristatus need to be reconsidered.

- The suggestion by Sharpe that Australasian Ospreys merit specific status deserves consideration.
- The position of ridgwayi in relation to carolinensis is unclear.

In this chapter I shall present data collected from museum specimens and discuss the variation in plumage and size of Ospreys. But before I proceed with the discussion of subspecies taxonomy, I shall review the paleontological record and the distribution of Ospreys, since these aspects can be relevant to subspecies definition.

1.2 METHODS

Osprey specimens were examined at:

American Museum of Natural History, New York
National Museum of Natural History, Smithsonian Institution
Peabody Museum of Natural History, Yale University
Museum of Natural History, Ottawa
British Museum (Natural History), Tring
Museum d'Histoire Naturelle, Paris
Naturhistoriska Riksmuseet, Stockholm

Natural History Museum at the University, Helsinki

In addition, H.J. de S. Disney was kind enough to send me measurements of Ospreys under his care at the Australian Museum, Sydney.

For each specimen, I measured wing length (flattened chord), tail length (from the tip to the uropygeum), the outside claw of each foot, and the culmen (from the tip of the bill to the base of the cere). I also scored the extent of markings on the crown on a scale of 1 to 3 (1- less than 10% black feathers, 2- from 10 to 50% black feathers, 3- more than 50% black feathers), and markings on the breast on a scale of 1 to 4 (1- breast almost white, 2- a band of partially brown feathers less than 3 cm wide, 3- a band of partially brown feathers more than 3 cm wide, 4- a wide band of entirely brown feathers).

Dr. D. Snow of the British Museum (Natural History), Tring, kindly gave me permission to relax skins in his care so that I could look at underwing coverts.

In the review of distribution that follows I will consider Ospreys as belonging to one species ocurring in four geographical areas: North America (carolinensis), Bahamas (ridgwayi), Palearctic (haliaetus, friedmanni and mutuus), and Australasia (cristatus, microhaliaetus and melvillensis).

1.3 LITERATURE REVIEW

1.3.1 NOMENCLATURE

Falco haliaetus, Linnaeus, Syst. Nat., 10 ed., 1758, P. 91 (Sweden)

Pandion fluviatilis, Savigny, Descr. de l'Egypte, Hist. Nat., 1, pp. 69, 95, 1809.

Pandion haliaetus, Lessieur, Man. d'Orn. I. p.86, 1828.

1.3.2 THE FOSSIL RECORD

According to Brunet (1970), and Harrison and Walker (1976), an Osprey, Paleocircus cuvieri, lived in Europe during the Upper Eocene, about 50 million years ago. The conclusion is based on partial remains of claws similar in shape to those of modern Ospreys, a shape unique in the class Aves. However, Warter (1976) disputes whether it was an Osprey, and suggests, based on more complete remains of wing bones, that Pandion homalopteron of the Miocene of California, about 13 million years ago, is the oldest known Osprey.

To judge from fossil remains, Ospreys lived during the Pleistocene throughout Western Europe, North America and the Bahamas (Lambrecht, 1933; Brodkorb, 1960).

1.3.3 THE DISTRIBUTION OF OSPREYS

1.3.3.1 Palearctic Ospreys

These Ospreys breed throughout the Palearctic from the Atlantic to

the Pacific (Figure 1.1), as far north as the timberline or even further north along forested river valleys in the tundra (Dementiev and Gladkov, 1951). In the boreal zone they nest mostly at inland sites while further south they are mainly coastal nesters. The southern limit is roughly at the tropic of Cancer, with populations extending further south to the Atlantic Islands (Cape Verde and Canary Islands) and along the Red Sea. Isolated instances of breeding have been reported in India and Burma (Ali and Ripley, 1968), but few of these have been confirmed. Sporadic breeding has also been reported in Africa (Mackworth Praed and Grant, 1962) but only one instance is accepted by Snow (pers. comm.), on the Berg River in South Africa, and even it might not be valid. As pointed out by Osterlof (1977), the presence throughout the year of sexually immmature birds may have given rise to reports of Ospreys breeding in East and South Africa (Mackworth Praed and Grant, 1952; Vaurie, 1965).

Palearctic Ospreys have suffered considerably from human persecution. In historical times they have disapeared from continental Western Europe and the Balkans (Bijleveld, 1974), and have been greatly reduced in numbers in the Islands of the Atlantic and Mediterranean, in Scotland, Eastern Europe and North Iran (Brown and Waterston, 1962; Bannerman, 1963; Osterlof, 1965; Bannerman, 1968; Bijleveld, 1974; Terrasse and Terrasse, 1977).

These Ospreys are migratory throughout most of their range: west Palearctic Ospreys wintering in West Africa (Osterlof, 1977),

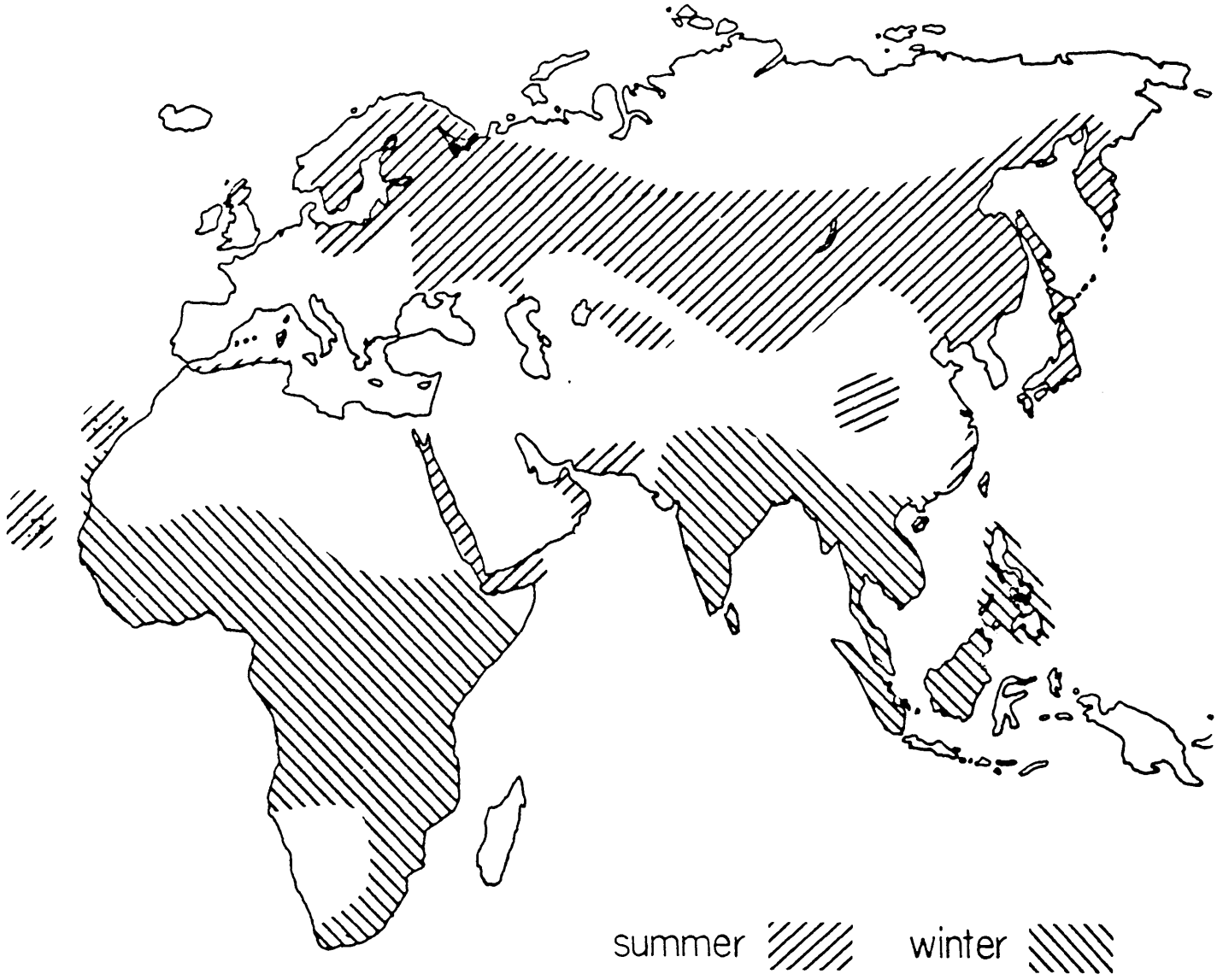

Figure 1.1 The breeding and wintering grounds of Palearctic Ospreys.

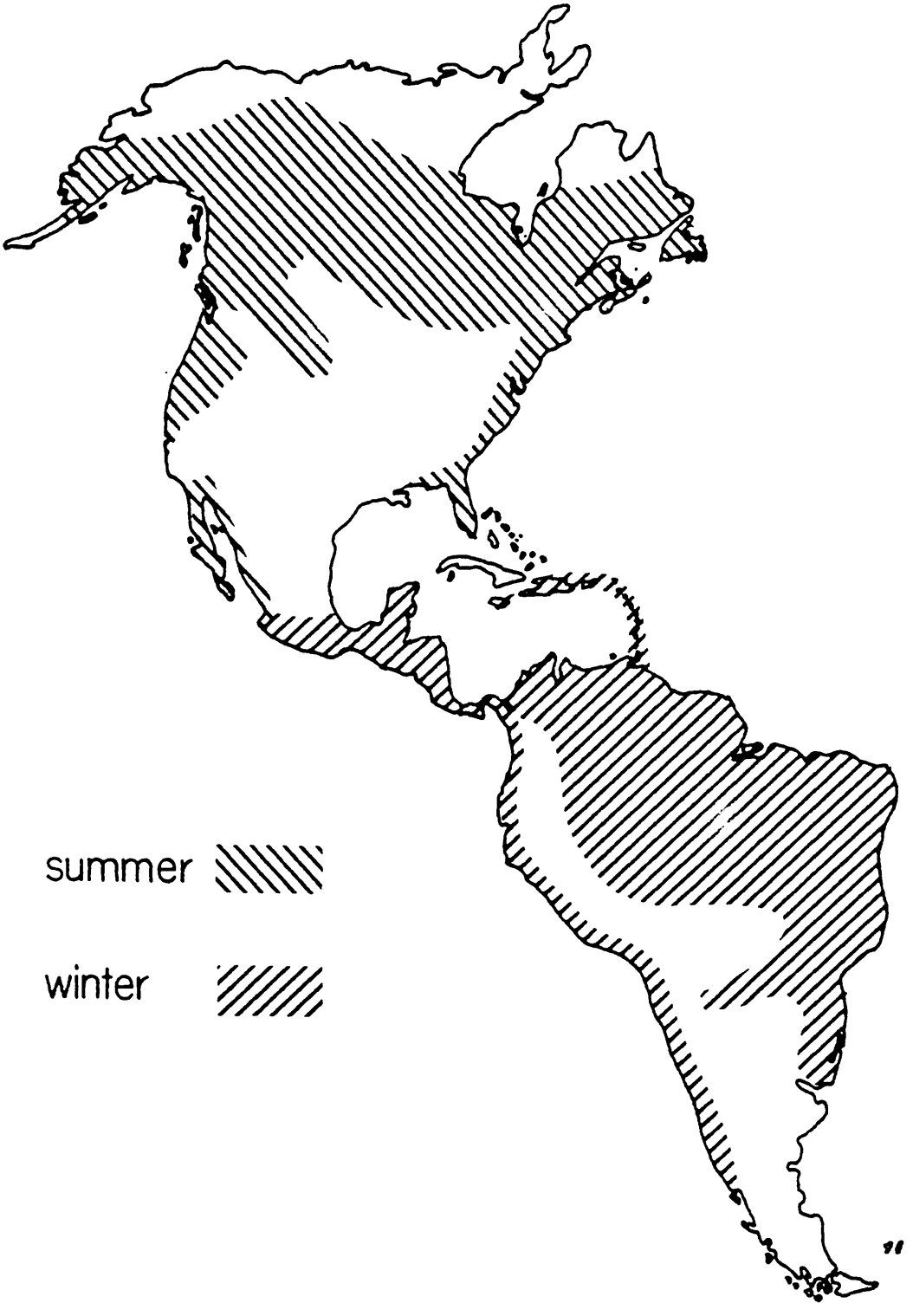

Figure 1.2 The breeding and wintering grounds of North American Ospreys.

Figure 1.3 The breeding grounds of Bahaman Ospreys.

Figure 1.4 The breeding grounds of Australasian Ospreys.

central Palearctic Ospreys in East Africa (Glutz Von Blotzheim, 1971) and east Palearctic Ospreys wintering in southern Asia, from India to the Philippines (Dementiev and Gladkov, 1951). However, Ospreys are year-round residents in the Atlantic Islands (Bannerman, 1963, 1968), along the Rea Sea (Smith, 1947, 1955; Clapham, 1964), in southern Iran (Hue and Etchecopar, 1970), and in south eastern China (Cheng, 1976; Seringhaus and Blackshaw, 1976).

1.3.3.2 North American Ospreys

These Ospreys occupy a similar range of habitats in North America as Ospreys do in the Palearctic (Figure 1.2). They breed south to South Florida in the east and to Sinaloa along the Pacific coast of Mexico. Although Ospreys have become locally extinct along the east coast (Henny, 1977), present distribution is thought to be similar to past one. This distribution in North America is disjunct, in great part because few breed along the Mississipi River or its tributaries, for reasons unknown. Land (1970) reported breeding in 1863 along the Pacific coast of Guatemala, but it is not known if this was by North American or Bahaman birds.

North American Ospreys are migratory throughout most of their range, wintering in Central and South America (Worth, 1936; Henny and Van Velzen, 1972; Kennedy, 1973; Melquist et al., 1979) as far south as Argentina and Chile, except for the populations of South Florida, Baja California and the Pacific coast of Mexico which are resident (Grinnell, 1928; Ogden, 1977; Henny and Anderson, 1979;

Westall, pers. comm.; Reitherman and Storrer, pers. comm.).

1.3.3.3 Bahaman Ospreys

These Ospreys breed in islands off Belize, in Quintana Roo, in islands off Cuba, in the Bahama Islands and perhaps on Hispaniola (Bond, 1971; Sprunt, 1977; Figure 1.3); they are resident throughout their recognized range.

1.3.3.4 Australasian Ospreys

These Ospreys breed in Australia including Tasmania, in the Lesser Sunda Islands, the Philippines, Celebes and Moluccas, Papua-New Guinea, and an arc of islands extending from the Bismarck Islands to New Caledonia (Figure 1.4). They do not breed in the rest of Melanesia, in New Zealand, or in the Greater Sunda Islands.

Australasian birds are thought to be resident, although Medway and Wells (1976) suggested that there was some migration from Australasia to Borneo and Java.

1.4 RESULTS

1.4.1 FEATHER MARKINGS

In all subspecies, the back and flight feathers of juveniles studied were tipped with white, giving the juveniles a speckled appearance which was lost in the first year through wear. In

Figure 1.5 The tail of juvenile (top) and adult (bottom) Palearctic Ospreys (Photo Yves Prevost).

Figure 1.6 The crown of juvenile (left) and adult (right) Palearctic Ospreys (Photo Yves Prevost).

addition, the tail of juveniles was more deeply barred and the crown was darker than in adults (Figures 1.5 and 1.6), two points already noted by Sharpe (1874).

Some of the most obvious variations between adults of different populations were in the crown and breast markings (Table 1.1). Crown markings differed between males and females but not in a consistent manner: Australasian males had significantly darker crowns than females (median test, chi-square=4.435, df=1, $p<.05$), North American males and females were not significantly different (median test, chi-square=2.262, df=1, $p>.10$), while Palearctic females were darker than males (median test, chi-square=8.286, df=1, $p<.01$). For both sexes, the crown markings of Palearctic and North American birds did not differ (males: median test, chi-square=1.047, df=1, $p>.30$; females: median test, chi-square=0.617, df=1, $p>.30$), but Australasian Ospreys had paler crowns (compared with Palearctic Ospreys, males: median test, chi-square=24.502, df=1, $p<.001$; females: median test, chi-square=65.406, df=1, $p<.001$) and Bahaman Ospreys had even paler crowns (sample size too small to test). In fact, some Bahaman Ospreys had a barely visible eye-stripe (Figure 1.7).

Macnamara (1977) established that the breast markings of North American Ospreys, are a secondary sexual character, most pronounced in females. This was also true for Palearctic and Australasian Ospreys (Table 1.1), although there was considerable overlap between the sexes. The only exception was the Bahaman Osprey in which neither sex had breast markings.

Figure 1.7 Head of the type specimen of Bahaman Osprey at at the British Museum (Natural History) (Photo Yves Prevost).

population	male				female			
	breast average		crown average		breast average		crown average	
Palearctic	2.7	(72)	2.5	(32)	3.4	(65)	2.7	(41)
Cape Verde	2.2	(6)	2.5	(6)	2.3	(4)	2.5	(4)
Red Sea	1.6	(5)	2.0	(5)	1.7	(3)	1.7	(3)
North American	1.4	(49)	2.6	(49)	2.4	(47)	2.8	(46)
Bahaman	1.0	(4)	1.0	(3)	1.0	(3)	1.0	(3)
Australasian	2.9	(42)	1.5	(42)	3.7	(50)	1.3	(50)

Table 1.1. Average breast and crown markings of Ospreys. From museum specimens. Sample sizes are in brackets.
The breast markings were scored from 1 to 4:

1 - breast almost white
2 - a band of partially brown feathers < 3 cm wide
3 - a band of partially brown feathers > 3 cm wide
4 - a wide band of entirely brown feathers

Crown markings were scored from 1 to 3:

1 - less than 10% black feathers
2 - from 10 to 50% black feathers
3 - over 50% black feathers

In both sexes of North American Ospreys, the breast markings were less pronounced than in Palearctic Ospreys (males: median test, chi-square=44.921, df=1, p<.001; females: median test, chi-square=40.343, df=1, p<.001) and the type of marking was different as reported by Baird et al. (1874):

> "In North American Ospreys the brown on the breast is in the form of detached faint spots, instead of a greyish brown wash, more or less continuous".

No North American female was found with a fully brown breast band (score of 4), while 55% of Palearctic females wore such a band.

Australasian Ospreys appeared to have darker breasts, but this was not significant (males: median test, chi-square=3.145, df=2, p>.20; females: median test, chi-square=3.759, df=2, p>.1).

Red Sea Ospreys appeared to have paler breasts and crowns than other Palearctic Ospreys, but a larger series than I examined would be necessary to show significance.

Sample sizes were sufficient to test whether juveniles from North America and the Palearctic differed in the intensity of the breast band according to sex, as in adults. Both sexes of juveniles had average scores intermediate beween those of adult males and females and these scores were not significantly different (Palearctic: median test, chi-square=2.955, df=2, p>.20; North America: median test, chi-square=4.955, df=2, p>.05). This result serves as a caution to any field workers

tempted to sex nestlings according to the intensity of the breast band.

1.4.2 SIZE

Ospreys also varied in size. As expected in a raptor, females in all populations were larger than males (wing length, tail length, bill length, claw size; $p<0.001$; Table 1.2). In both sexes, Palearctic Ospreys had shorter wings, bills and claws than North American birds ($p<.001$), but tail length was not significantly different ($p>.20$). Within Palearctic Ospreys, the non-migratory Red Sea form had smaller wings and tail than the migratory form, but the sample size was too small to test statistically. The same applied to the resident Bahaman Ospreys when compared with the migratory North American Ospreys, but here again samples were too small to test statistically. However, no such trend was apparent in the resident Cape Verde Ospreys, when compared to migrant Palearctic birds.

The resident Australasian Ospreys had the shortest wings and tails ($p<.001$, when compared to Palearctic Ospreys), with females shorter than males of the other populations.

Resident tropical populations had longer and thinner claws relative to their size than did migrant Ospreys, in accordance with Allen's ecogeographic rule that appendages are longer at low latitudes (claws were a relevant appendage because they are vascularized and Allen's rule is thought to be related to heat

population	sex	N	wing length in mm +-s.e.	tail length in mm +-s.e.	bill length in mm +-s.e.	claw size in mm +-s.e.
Palearctic	male	(72)	474+-11	210+-9	314+-12	277+-11
	female	(77)	496+-15	226+-9	336+-15	289+-11
Cape Verde	male	(7)	479+-14	218+-7	331+-13	309+-10
	female	(4)	490+-10	241	333+-14	312+-13
Red Sea	male	(5)	464+-16	199+-10	308+-13	284+-17
	female	(3)	477+-20	219	338+-26	305+-11
North America	male	(49)	485+-12	212+-8	325+-12	289+-10
	female	(47)	507+-10	228+-6	346+-13	305+-12
Bahama	male	(4)	461+-7	-	335+-3	322+-1
	female	(3)	492+-26	225+-12	361+-17	326+-10
Australasia	male	(42)	418+-17	181+-8	304+-12	284+-13
	female	(50)	442+-15	195+-10	328+-14	299+-12

Table 1.2. Average wing, tail, bill and claw measurements of Ospreys. From museum specimens.

locality	wing lengths in mm			
	males	(N)	females	(N)
New Caledonia	405+-10	(3)	424	(1)
Bismarck and Solomon Islands	409+-11	(9)	444+- 9	(10)
Papua-New Guinea	413+-10	(12)	444+- 9	(10)
Celebes, Moluccas and Lesser Sundas	417+- 6	(4)	445+-11	(3)
Philippines	454	(1)	-	
West Australia	430+-10	(3)	449+-18	(3)
North Australia	409+-12	(5)	451+-14	(7)
South Australia	-		479	(1)

Table 1.3. Comparison of the average wing length of Australasian Ospreys from various localities. One male specimen (wing= 440mm) excluded for New Caledonia and 6 clearly wrongly sexed specimens (4 females and 2 males) excluded for the Celebes, Moluccas and Lesser Sunda Islands.

dissipation). In particular, Cape Verde Ospreys had longer claws than Palearctic migrants (males: $t=7.807$, $df=84$, $p<.001$; females: $t=3.357$, $df=79$, $p<.001$), Australasian Ospreys than the much larger Palearctic migrants (males: $t=2.976$, $df=129$, $p<.01$; females: $t=4.885$, $df=131$, $p<.001$) and Bahaman Ospreys than the larger North American migrants (males: $t=41.218$, $df=54$, $p<.001$; females: $t=2.652$, $df=49$, $p<.02$)

As noted by Knowlton and Ridgway (1909), Bahaman Ospreys had "much larger and more swollen" bills but sample sizes were too small to test statistically.

There was also a size variation within Australasian Ospreys, those from Australia itself being slightly larger than the rest of the population (Table 1.3). In my sample, this was significant for females ($t=2.19$, $p<0.05$, $df=43$), but not for males ($t=1.55$, $p>.1$, $df=34$).

1.4.3 UNDERWING COVERTS

Because of the large overlap of breast and crown markings between populations and sexes, I could not fully discriminate populations by using these characters. I searched for a more diagnostic character, and found that underwing coverts varied little within populations but considerably between populations. For all populations, the underwings of juveniles were very similar (Figure 1.8): in all cases the primaries, secondaries and their respective coverts were barred; Palearctic juveniles were indistinguishable from North American

juveniles, while Bahaman and Australasian juveniles only differed from these in the lesser coverts.

In all populations the underwing coverts of adults were less barred than those of juveniles. In Palearctic adults, the only variation in residents and migrants from West Europe to Japan was that Red Sea adults had paler secondary underwing coverts. However, all Palearctic adult Ospreys - and only these - had the larger underwing coverts one half rufous-brown, one half white (Figure 1.9), and although North American Ospreys had underwings very similar to those of Palearctic Ospreys, their larger underwing coverts were barred dark brown. In Bahaman Ospreys these coverts were nearly white, while in Australasian birds they were nearly all ashy brown.

The underwings of Bahaman Ospreys (Figure 1.10) were like the underwings of very pale Palearctic or North American Ospreys, but the underwings of Australasian Ospreys (Figure 1.11) were different from that of the other three: the primaries and secondaries were barely barred, the primary coverts were fully brown, and the secondary coverts had a thin brown line along the rachis, a pattern far more removed from the juvenile pattern than were the patterns of Palearctic, North American or Bahaman Ospreys.

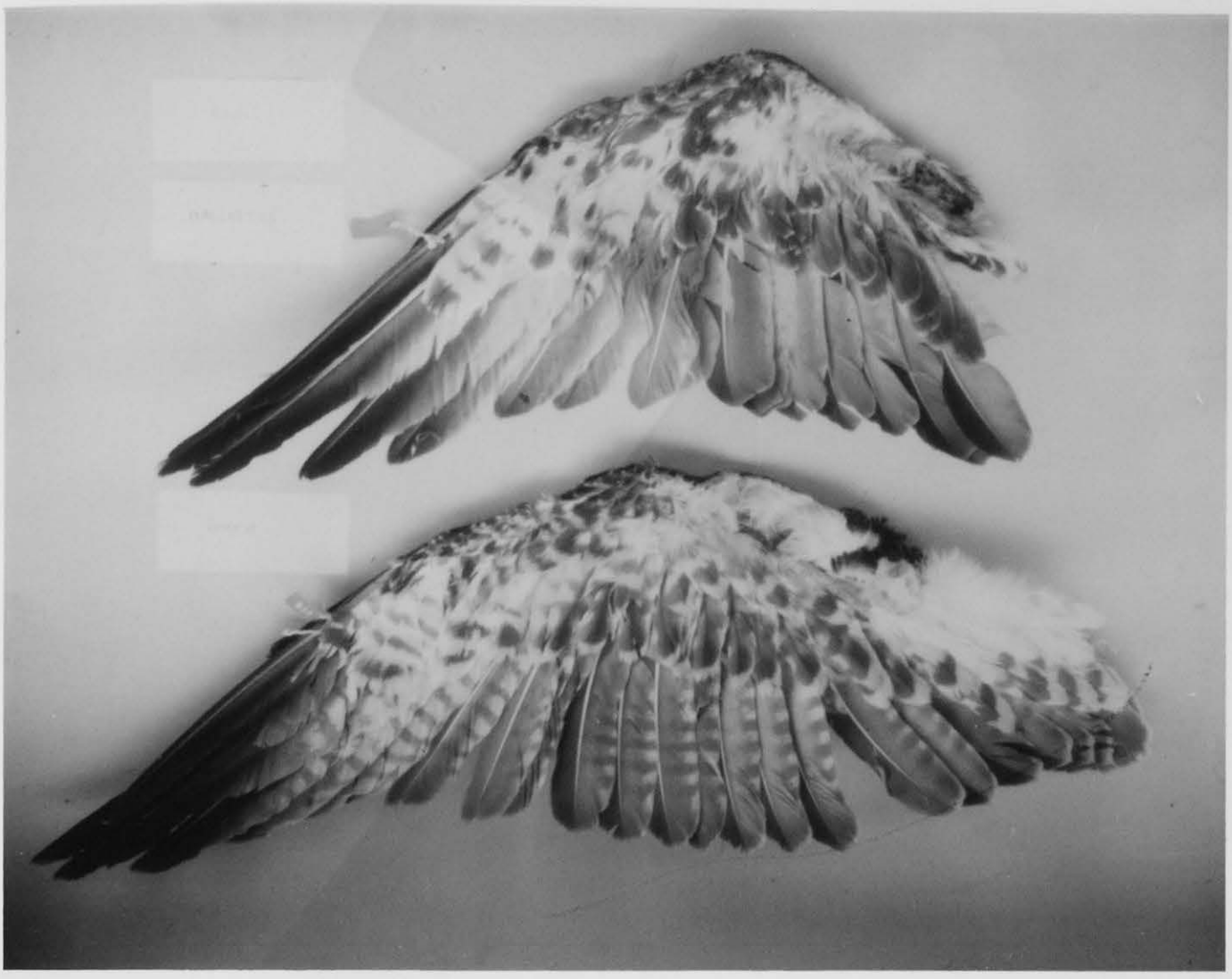

Figure 1.8 Underwing of juvenile (bottom) and adult (top) Palearctic Ospreys (Photo Yves Prevost).

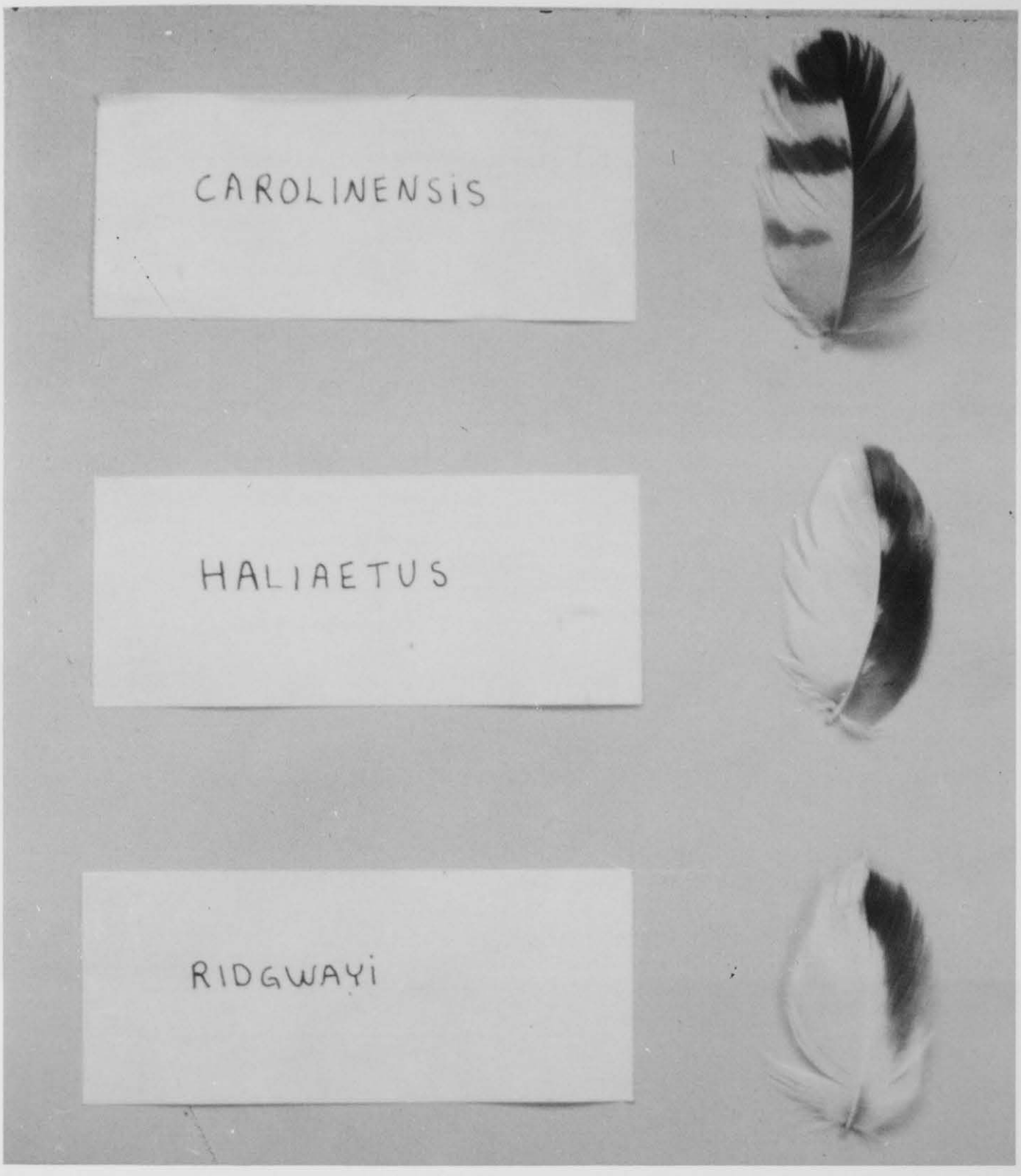

Figure 1.9 Underwing primary coverts of North American (top) Palearctic (middle) and Bahaman (bottom) Ospreys (Photo Yves Prevost).

Figure 1.10 Underwing of Bahaman Osprey
(Photo Yves Prevost).

Figure 1.11 Underwing of Australasian (bottom) and Palearctic (top) adult Ospreys (Photo Yves Prevost).

1.5 DISCUSSION

1.5.1 OSPREY SUBSPECIES

Palearctic and North American Ospreys were distinguished on the basis of differences in breast markings (Baird *et al.*, 1874). However, Baird *et al.* (1874) stated:

> "While in consideration of the above facts, I am for the present compelled to recognize the American *Pandion* under the distinctive name of *carolinensis*, I may say, that, if any European birds occur with the breast immaculate, - no matter what proportion of specimens, - I shall at once waive all claims to the distinctness of the American bird."

The variation in Palearctic Ospreys was such that some males did have immaculate breasts. However, differences in the lesser primary coverts of the underwing showed that Palearctic Ospreys were distinct from North American Ospreys and that *haliaetus* and *carolinensis* were valid subspecies representing separate breeding populations.

Wolfe (1946) did not seem to be aware of the sexual dimorphism in the breast markings, and stated that Manchurian Ospreys, *friedmanni*, had darker breast markings than other Palearctic Ospreys. Contrary to him, I have seen skins from the west Palearctic (always females)

with solid brown breast bands. There was no geographical separation on breast markings for Palearctic Ospreys, except for Red Sea Ospreys; on the other hand there was considerable variation at all localities within the range. I believe that friedmanni is only a synonym of haliaetus.

Kipp created the subspecies mutuus based on the small winglength of two adult males (440 and 442 mm) from Foochow in South China. I did not examine any adult males from this locality. However, two juvenile males from Foochow (BMNH 1908-1436 and AMNH 536617) had wing lengths (right wing) of 474 and 489 mm; in addition, an adult female from Foochow (BMNH 1902-85367) had a wing length of 497 mm. These values fall well within the range for other Palearctic Ospreys showing that the specimens examined by Kipp were not truly representative of Foochow. I believe that mutuus is only a synonym of haliaetus.

According to Bergman's rule, subtropical and tropical resident Ospreys should have smaller bodies than northern migratory ones, while according to Gloger's rule subtropical and tropical Ospreys should be paler than northern ones. This is the case with Red Sea Ospreys, and the opinion of Kipp exaggerated this trend for south China Ospreys. However, if the smaller size, and paler breast and crown markings of Red Sea Ospreys are used to define them as a separate subspecies, then I feel that all resident populations in the Palearctic and North America should also be given subspecific status. Each of these is as distinct a breeding population from

migratory populations as Red Sea Ospreys are from other Palearctic Ospreys. Subspecies would then be assigned on migratory habits. I refuse to do this because it overemphasizes the distinctness of these resident populations relative to migratory ones.

Australasian Ospreys were sufficiently different morphologically from other Ospreys to warrant at least subspecific status, but if they are to be split into two subspecies according to size, then it should be along a line north of Australia rather than at latitude 20 South as in Vaurie (1965). Although males from North Australia were on average smaller than males from West Australia, females were not; however both were on average larger than Ospreys from the rest of Australasia (not significant for males). If the boundary between subspecies is moved north then the proper subspecies name for the smaller Osprey would revert to microhaliaetus, Brasil 1916; it would remain cristatus for the larger form. However, I reject the subspecific distinction because there was considerable overlap between Ospreys north and south of this line (as already pointed out by Hartert, 1923), and because it overemphasizes differences within Australasian Ospreys when compared with Palearctic, North American and Bahaman birds. If subspecies are recognized within Australasian Ospreys, I believe it will then be necessary to consider Australasian Ospreys as a separate species, Pandion cristatus, Vieillot 1816, so as to convey the difference between Australasian and other Ospreys. This species would have two subspecies, Pandion cristatus cristatus, in the south and Pandion cristatus

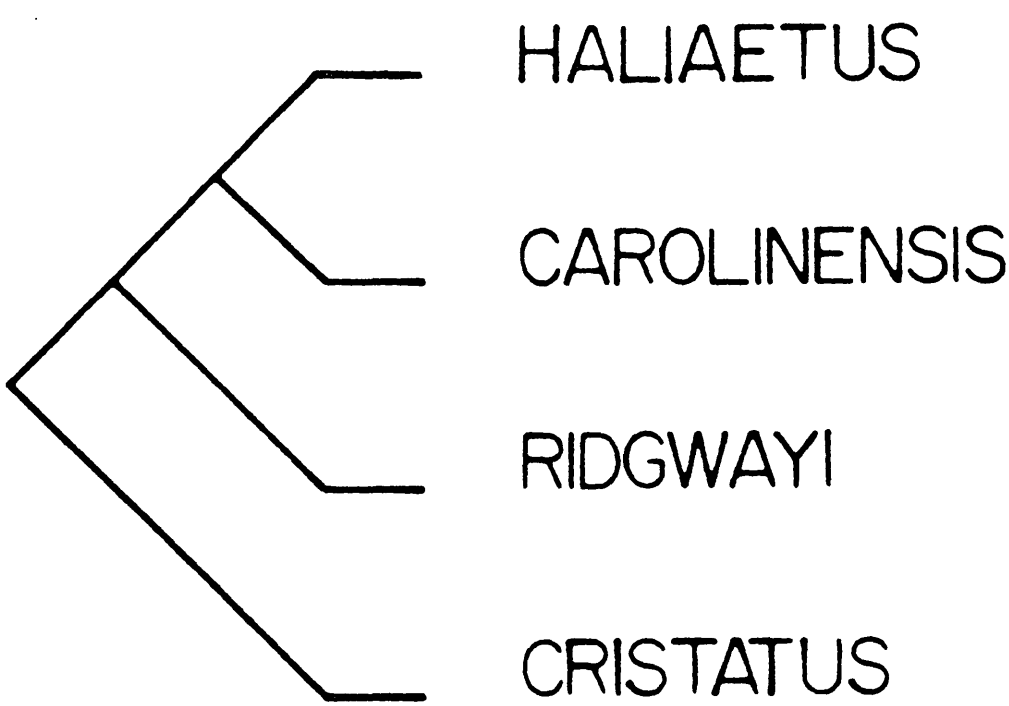

Figure 1.12 Affinities between Osprey subspecies.

microhaliaetus, in the north.

In conclusion, I recognize four subspecies, haliaetus, carolinensis, ridgwayi and cristatus, corresponding to Palearctic, North American, Bahaman and Australasian Ospreys. The affinities between these are illustrated in Figure 1.12: cristatus is the most distinct, ridgwayi is closer to haliaetus and carolinensis than to cristatus, and haliaetus and carolinensis are most alike.

1.5.2 RELATIONSHIP AMONG THE SUBSPECIES

Ospreys evolved at such an early date that subsequent shifts in their distribution erased most of the clues as to the center of origin of recent Ospreys (Mayr, 1946). Consequently, detailed scenarios are mere speculation. Nevertheless, a few points can be made.

The morphological differences between Palearctic and North American Ospreys were so small that there probably was gene flow between these two populations during the Pleistocene. The possibilities of gene flow between the Palearctic and North America are presently minimal because Ospreys do not breed in the vicinity of the Bering Strait, the major path of flow. However during the climatic optimum, about 8000 years ago (Moreau, 1972), Ospreys certainly bred further north than at present, including both sides of the Bering Strait, and opportunities for gene flow were much greater. Presumably, such opportunities also occurred during each of the previous interglacials.

The morphological similarities between migrant and resident Ospreys within the Palearctic and within North America suggests that the separation between migrants and residents is more recent than the separation between North American and Palearctic Ospreys, and prohibit the assignment of subspecies according to migratory habits.

At the peak of glaciations habitat types were shifted south, and the area of seasonal weather (north of the tropic of Cancer) suitable for breeding was much less than at present. Therefore, it was the number of migrant Ospreys which decreased, rather than the number of resident Ospreys. Migrant and resident populations were probably in closer geographical contact, and the distinction less marked, than at present. As the weather improved, Ospreys reoccupied the north-temperate zone while reacquiring migratory habits.

The relationhip between Bahaman Ospreys and the other subspecies remains unclear. They could be the remains of a previous North American population subsequently displaced by Ospreys from the Palearctic, these forming the present North American population, or they could be a recent offshoot from North American Ospreys, better adapted to breeding in subtropical habitats. In any case, there is apparently secondary contact between the two populations in the Everglades of South Florida: some of the Ospreys breeding there have pale heads and immaculate breasts like Bahaman Ospreys (Allen, 1962; Ogden, 1977; Poole, pers. comm.) while others have the darker crowns and breast bands of North American Ospreys.

According to Voous (1960):

> "on grounds of geographical variation, the distribution offshoots in the tropics may be regarded as of considerable antiquity".

Based on plumage and size this appears to be true of Australasian Ospreys but not of Bahaman Ospreys or of other populations of resident Ospreys found just south of populations of migrants. Basically there are two Ospreys: an Holarctic Osprey, of which the Bahaman Osprey is a slightly modified form, and the Australasian Osprey. The wintering ranges of these two Ospreys overlap in the Philippines (Dupont, 1971), but their breeding ranges are distinct though only 400 km apart at their nearest point from Taiwan to the Philippines.

These two Ospreys are at present best treated as one species but future work, such as electrophoresis or DNA-DNA hybridization, might show that they are distinct species. Such work might also answer whether Bahaman Ospreys are closely related to North American Ospreys.

CHAPTER 2

THE DISTRIBUTION AND ABUNDANCE OF OSPREYS IN SENEGAMBIA

2.1 INTRODUCTION

The European Osprey, *Pandion haliaetus haliaetus*, has been extensively studied in its breeding area, yet practically nothing is known about its biology on the wintering grounds. Osterlof (1951, 1977) has shown from banding returns that most European Ospreys winter in West Africa (Figure 2.1) and that immatures return to Europe only at two or three years of age. Numerous bird lists confirm Osterlof's results but no study has been made of habitat, food and densities of Ospreys on their wintering grounds.

For reasons of logistics, I chose to work in Senegambia where prior reports had shown that Ospreys wintered in all wetland habitats including coastal beaches, mangrove forests, and inland rivers and lakes (Cawkell and Moreau, 1963; Cawkell, 1964; Morel and Roux, 1966; Thiollay and Dupuy, 1970; Dupuy, 1972, 1973; Morel and Roux, 1973).

In this chapter I shall document habitat preferences and population densities of Ospreys in Senegambia, while in the next chapter I shall discuss food and foraging.

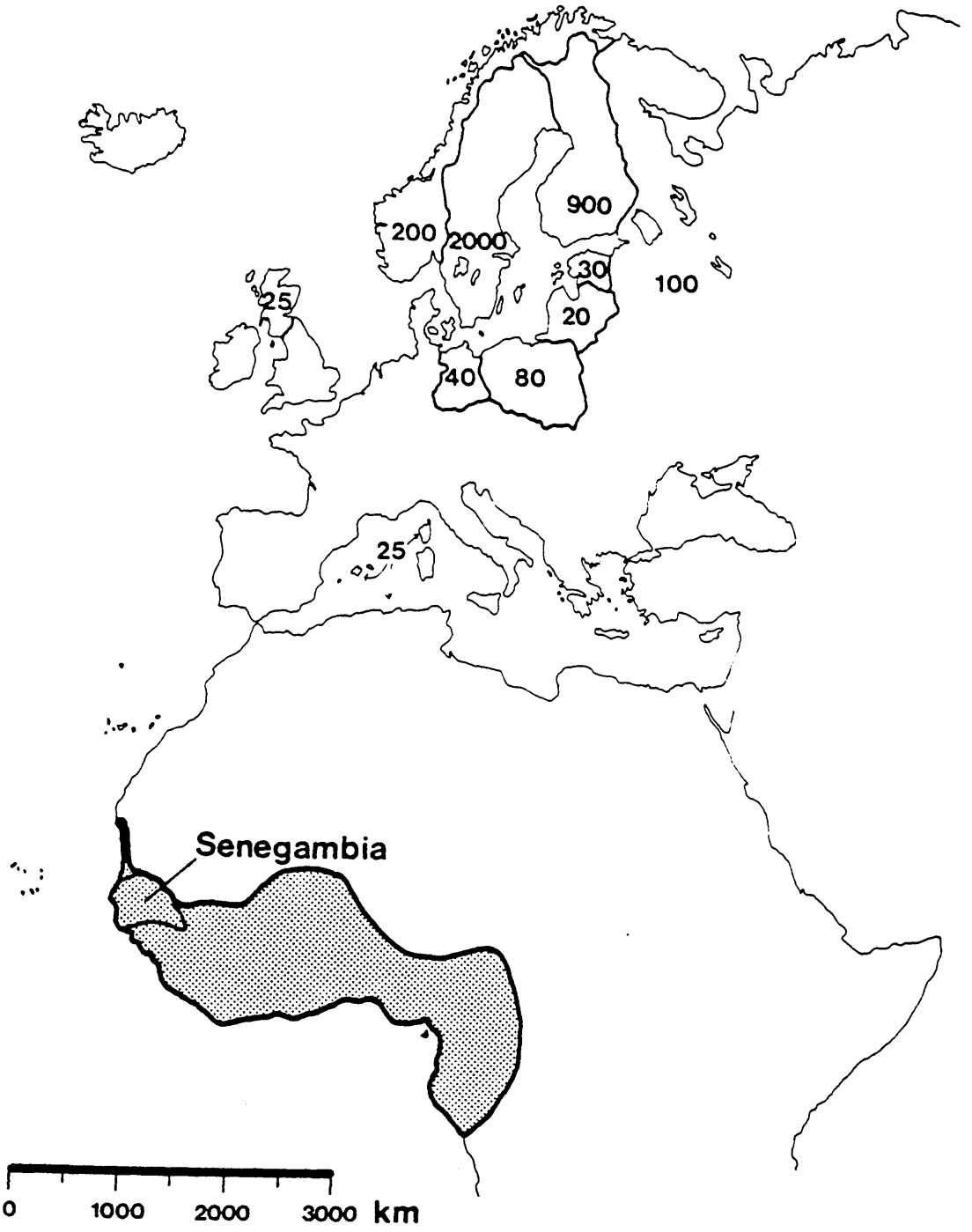

Figure 2.1. Wintering grounds of European Ospreys and the number of breeding pairs in Europe. Adapted from Osterlof (1977) and Terrasse and Terrasse (1977).

2.2 STUDY AREA

Senegambia lies at the extreme western side of Africa between 12 and 17 degrees latitude north. Four major rivers cut the landmass (Figure 2.2): the Senegal, Saloum, Gambia and Casamance. The Senegal and the Gambia Rivers are of tropical type, with floodwaters provided by rainfall in the upper basins; the floodwaters of the Senegal River are sufficient to make waters at sea fresh and opaque with silt. The river has a wide floodplain with numerous lakes, ponds and tributaries. Downstream from this floodplain, the river follows a thin sandspit for 20 km and then flows into the sea through a narrow outlet.

The Casamance, and particularly the Saloum, deltas receive much less floodwater and are little more than intrusions of the sea into the landmass. These deltas support extensive mangrove forests, each of which is drained by its own network of channels. The lower part of the Gambia River also supports extensive mangroves, but only remnants of mangrove are found at the mouth of the Senegal River.

At the tip of the Cap-Vert peninsula, where the city of Dakar is located, there is a rocky coast of volcanic origin, and to the south, between Bargny and the Somone River, there are irregular sandstone outcrops and cliffs. Elsewhere, the coast is made of low beaches with small rocky outcrops near MBour, Pointe Gaskel, at the mouth of the Gambia River and south of the Casamance River mouth. South of the Cap-Vert peninsula, these beaches form a succession of

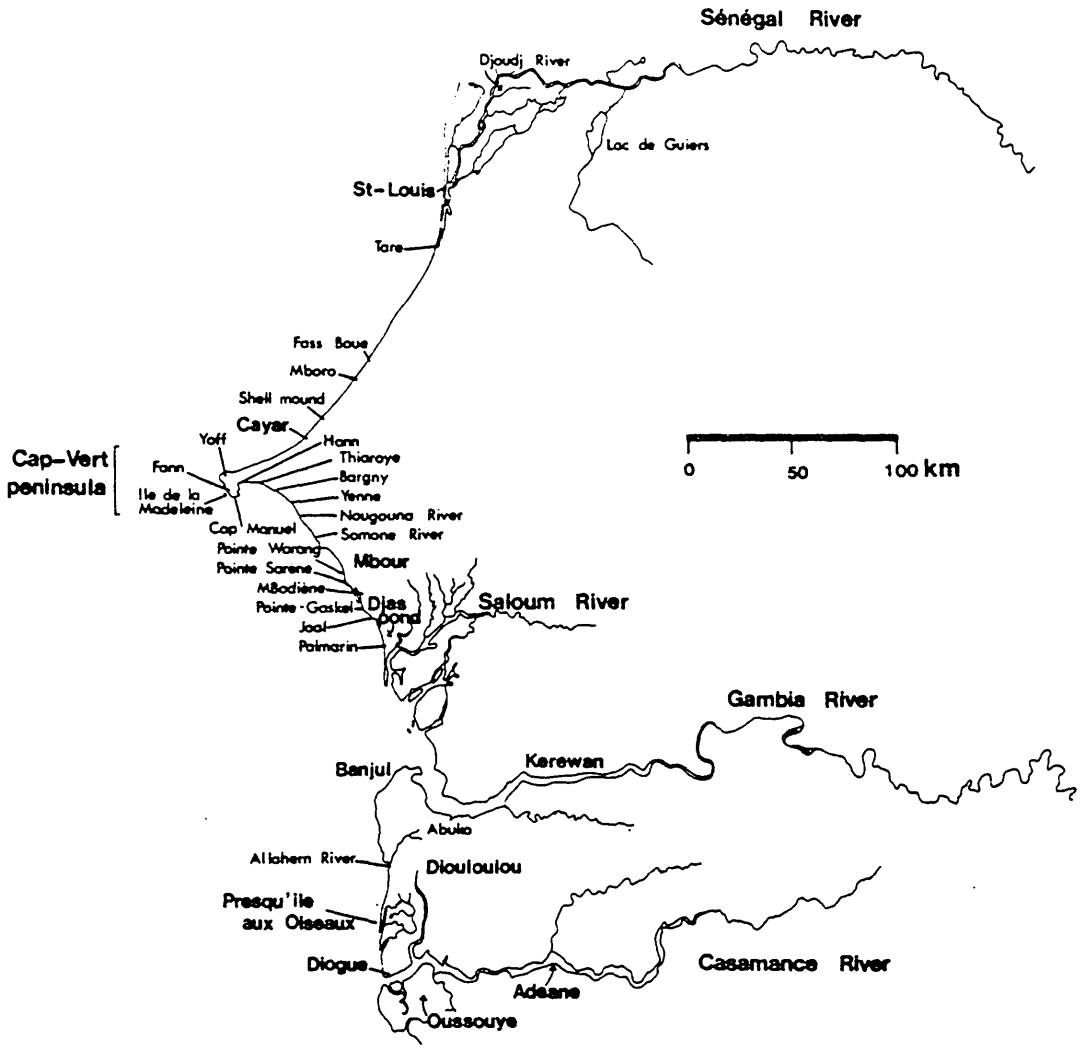

Figure 2.2 Map of Senegambia.

coves usually bordered by trees and interrupted by riverbeds dry outside the rainy season. North of the peninsula, the beaches are bordered by barren sand dunes extending inland for several kilometers, and are uninterrupted for the 170 km to the mouth of Senegal River.

The physionomy of the sea bottom along the coast also varies (Domain, 1976). North of the Cap-Vert peninsula, the continental shelf is narrow and at the level of Cayar a deep trench cutting through it almost reaches the shore; the zone of waters less than 5 m deep consists of a narrow band along the shore less than 100 m wide and wave action is strongly felt. South of the peninsula, the continental shelf is wide; the zone of shallow waters extends 5 to 15 km out to sea, and breaks the force of the waves, resulting in a sheltered environment despite the open nature of the coast. However, in the vicinity of the Saloum, Gambia and Casamance River mouths the beaches are generally more exposed.

Between the Cap-Vert peninsula and the Saloum River, especially between Joal and Palmarin, pockets of fresh water are trapped during the rainy season and gradually evaporate in the following months while increasing in salinity, sometimes completely drying up. Some of these ponds drain out to sea and fish migrate into them when they are full of water but return to sea as they dry.

There are three main seasons: (1) cold and dry, from December to March, (2) hot and dry, from April to June, (3) and hot and wet, from July to November. Seasonal characteristics vary with latitude,

the north being on average cooler and drier.

I will use the term `winter' for the time when adults were present (from mid-October to mid-March) and `summer' for the time when they were absent (mid-April to mid-August). Unless otherwise specified, survey results are from winter.

Sea waters from the Canary Islands and the Guinea meet off the coast of West Africa, the position of the point of contact varying seasonally. From November to March, the Canarian waters, accompanied by strong westerly winds, bring rough seas and water temperatures as low as 16 degrees C in northern Senegambia. From March onwards, these waters are gradually replaced by Guinean waters as the front moves from the south of Senegambia to the north of Senegambia, where it remains from June to October. The Guinean waters, accompanied by light easterly winds, bring flat seas and water temperatures as high as 26 degrees C.

2.3 METHODS

Surveys of Ospreys were done to get minimum estimates of Osprey numbers and to compare numbers between habitats. An extensive survey was done in the winter of 1977-78. In 1978-80, selected areas were surveyed in greater detail and Ospreys were colour-marked to determine whether they were sedentary on their wintering grounds, and the extent of their ranges.

During surveys I made use of the fact that Ospreys were conspicuous birds that perched in prominent places and that most birds in an area could be seen from far away. However, since surveys were made at different times of day, the results might be biased because of movements to or from sites during the day.

The entire coast (440 km) was surveyed between 3 January and 22 February 1978 except for built up areas near Dakar, MBour and Banjul, and 20 km of coast north of the Casamance River mouth. Beaches were surveyed with a Land Rover when possible, otherwise on foot; Ospreys were counted as they were overtaken.

Selected areas of mangrove were surveyed using motorboats, and linear projections were made to estimate numbers in the unsurveyed areas. Although these areas were selected because of their ease of access, I believe they are representative samples. Care was taken not to count birds twice and to account for possible movements. As a result of the method, Osprey numbers were probably underestimated.

Ospreys were captured using a snare powered by a thin strip of inner tube. The trap mechanism is described in an Appendix. I captured 120 different Ospreys, and of these 15 were captured twice, 5 were captured three times and 1 was captured five times. Captured Ospreys were marked with patagial tags made from Darvic in a choice of seven colours. Tags on left wings identified the locality:

orange: north of the Senegal River mouth

yellow: south of the Senegal River mouth

green: coast between the Senegal River mouth and the Cap-Vert peninsula

red: Djas pond

blue: mouth of the Saloum River

lime: Saloum River delta

white: Saloum River delta

Tags on right wings identified the age class: white for Ospreys hatched in 1979; red, orange and yellow for Ospreys hatched in 1978; lime, blue and green for Ospreys hatched prior to 1978. A colour leg ring identified individuals within age classes at a site, and a metal ring from the Museum d'Histoire Naturelle de Paris provided a more permanent reference. The locality where a bird was marked and its age class could be determined from patagial tags at distances up to 1 km with binoculars or a 20-60X telescope. However, individuals, determined from colour rings, could only be identified from less than 200 m on clear days.

At least five Ospreys lost one or more patagial tags during the study; however, most Ospreys kept their tags. Only one Osprey lost a colour ring. None were known to lose metal rings.

2.4 RESULTS

2.4.1 SENEGAL RIVER VALLEY

Two Ospreys were observed at the Lac de Guiers on 7 January 1978, where up to five had been seen by previous observers (Treca, pers. comm.).

Two surveys were conducted along the Senegal River from the Djoudj River to St-Louis (Figure 2.3). On 22 February 1978, 8 Ospreys were seen, while on 22 February 1979, 17 Ospreys were seen, 7 of them on exposed mud flats 5 km north of St-Louis. The second survey was extended to include mud flats south of St-Louis where an additionnal 27 Ospreys were observed.

The results of surveys north and south of the river mouth fluctuated greatly (Figure 2.4). Nevertheless, they permitted a rough estimate of the minimum number of Ospreys in the area. This reached 29 south of the river mouth and 42 north of the river mouth in winter, but only 1 south of the river mouth and 6 north of the river mouth in summer.

If we sum the figures and make a projection for similar habitats in the unsurveyed part of the Senegal River upstream from the Djoudj River, then at least 25 Ospreys wintered in the Senegal River valley upstream from St-Louis and about 100 wintered downstream from St-Louis.

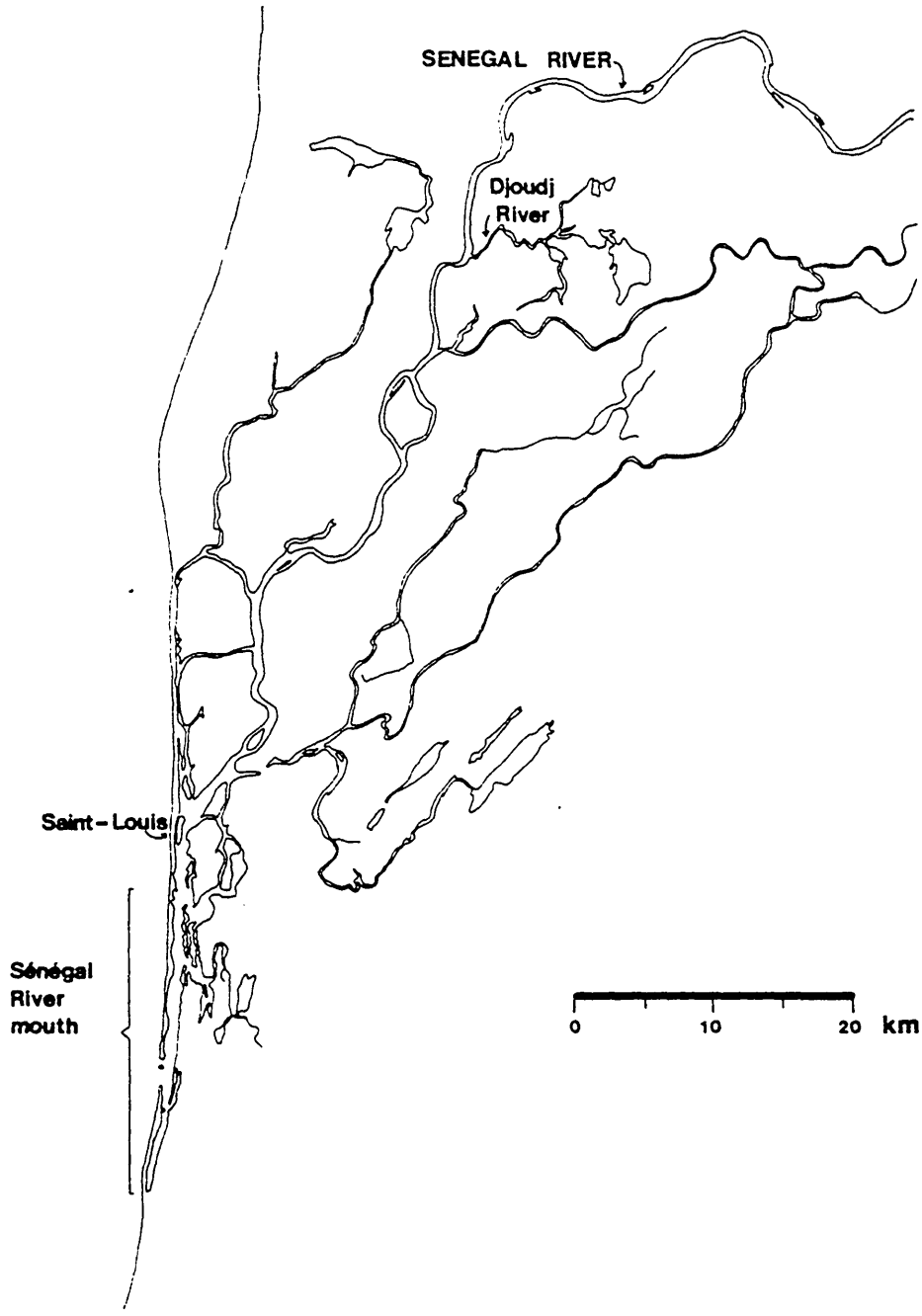

Figure 2.3 Senegal River Valley.

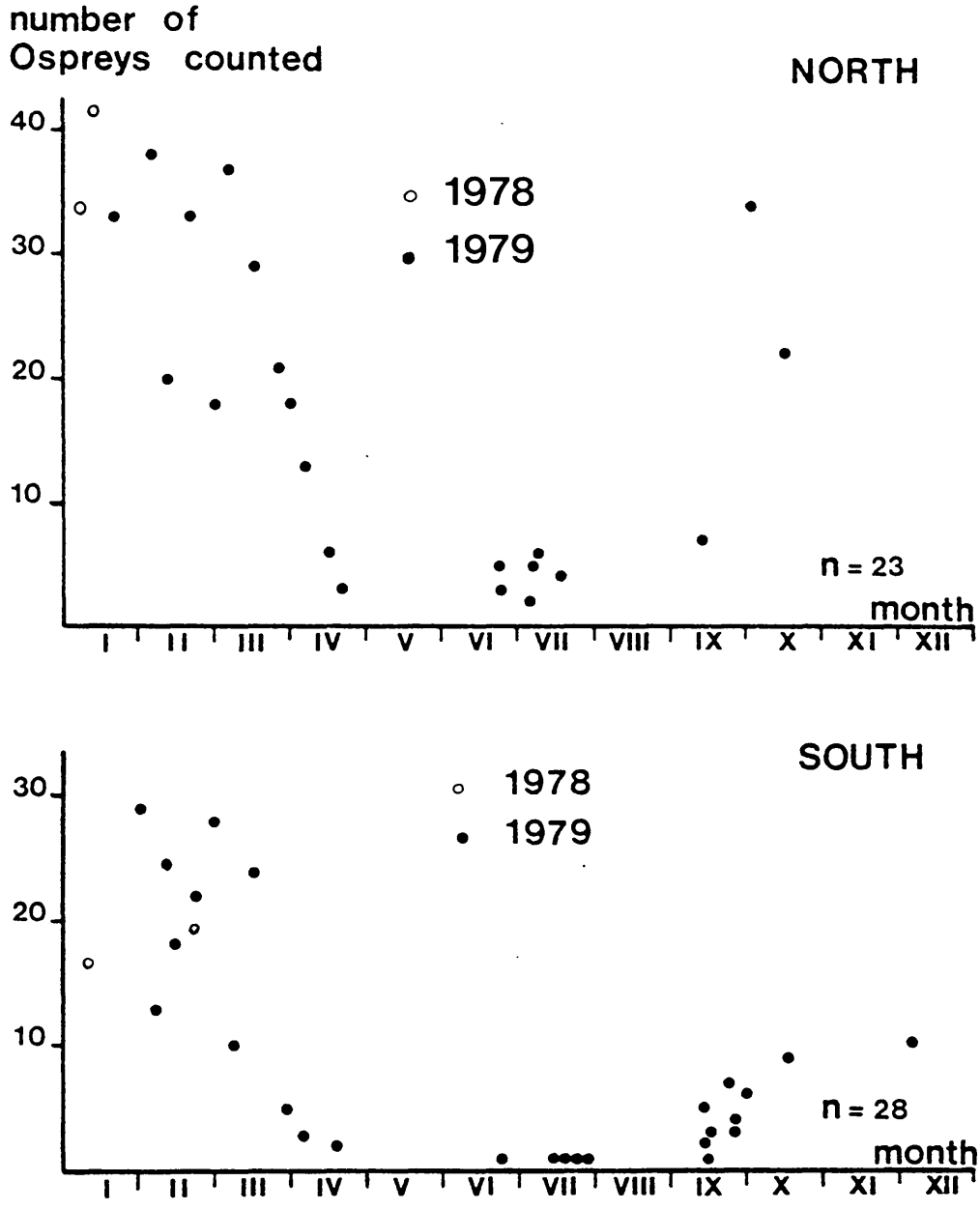

Figure 2.4 Results of surveys conducted north and south of the mouth of the Senegal River.

2.4.2 COAST BETWEEN THE SENEGAL RIVER MOUTH AND THE CAP-VERT PENINSULA

A maximum of 76 Ospreys was counted along the coast between the mouth of the Senegal River and the Cap-Vert peninsula (Table 2.1; Figure 2.2). Almost all Ospreys were observed between Yoff and Fass Boue (91 km) and very few between Fass Boue and the Senegal River mouth (63 km). There was only one point of concentration, a shell mound north of Cayar where 4-8 Ospreys were observed. No Ospreys were observed in June along the coast and no fresh remains of fish were found then at any of 17 feeding perches earlier used by Ospreys, while only one Osprey was seen on 1 August between Yoff and the shell mound.

2.4.3 CAP-VERT PENINSULA

There were two points of focus: (1) the Dakar-Yoff airfield where 10 Ospreys were observed on 11 December 1977 resting on bushes and on the airstrip, and 8 were counted on 19 February 1978; and (2) on Ile de la Madeleine where 5 Ospreys were observed perching and roosting on the top of cliffs on 30 November 1977. Individual Ospreys were observed foraging between Fann and Cap Manuel and between Hann and Thiaroye. I estimate at least 20 Ospreys wintered on the Cap-Vert peninsula.

locality	distance in km	1978				1979			
		3/01	20/02	29/01	22/02	14/03	20/06	11/09	22/11
Yoff-end of trees	32	13	20	9	26	-	-	-	-
End of trees-Cayar	8	5	3	4	8	7	0	1	4
Cayar-shell mound	13	4	2	7	8	5	0	1	9
Shell mound	2	6	4	6	6	3	0	3	8
Shell mound-MBoro	24	20	11	22	22	17	0	2	25
MBoro-Fass Boue	12	3	1	1	2	0	0	0	-
Fass Boue-Tare	63	2	2	5	4	2	0	0	-

Table 2.1. Ospreys counted on different dates between the mouth of the Senegal River and the Cap-Vert peninsula.

2.4.4 COAST FROM THE CAP-VERT PENINSULA TO THE DJAS POND

On 15, 16 and 17 January 1978, 26 Ospreys were observed regularly distributed along the coast (Table 2.2). North of the Somone River they fed and rested on open salt flats while south of the Somone River they more often perched on trees away from the coast.

2.4.5 DJAS POND

Up to 32 Ospreys were counted on the salt flats surrounding the Djas pond (an area about 15 km square, see Figure 2.5) and 7 during summer.

2.4.6 SALOUM RIVER DELTA

In the Saloum River delta Ospreys were found in a range of habitats, from sandy beaches to offshore islands and closed mangrove (Figure 2.5). Counting was complicated by Osprey movements between these habitats in relation to tides. The ebbing tide exposed mud flats in the mangrove, reducing the area available for foraging and removing the possibility to forage while perched from a tree along a channel. In response, Ospreys were observed at ebbing tide flying from closed mangrove to the coast or to more open mangrove where they foraged in the large channels that remained flooded, and at rising tide returning to closed mangrove. Thus the number of Ospreys observed in closed mangrove was highest at high tide while along the coast and in estuaries it was highest at low tide.

locality	27 and 28 December 1977	15,16 and 17 January 1978
Yenne-Bope	-	5
Nougouna River	-	4
Somone River-MBour	7	5
Warang Point	2 (22 December)	2
Sarene Point	-	3
MBodiene-Pointe Gaskel	5	7

Table 2.2. Ospreys counted on different dates between the Cap-Vert peninsula and the Djas pond.

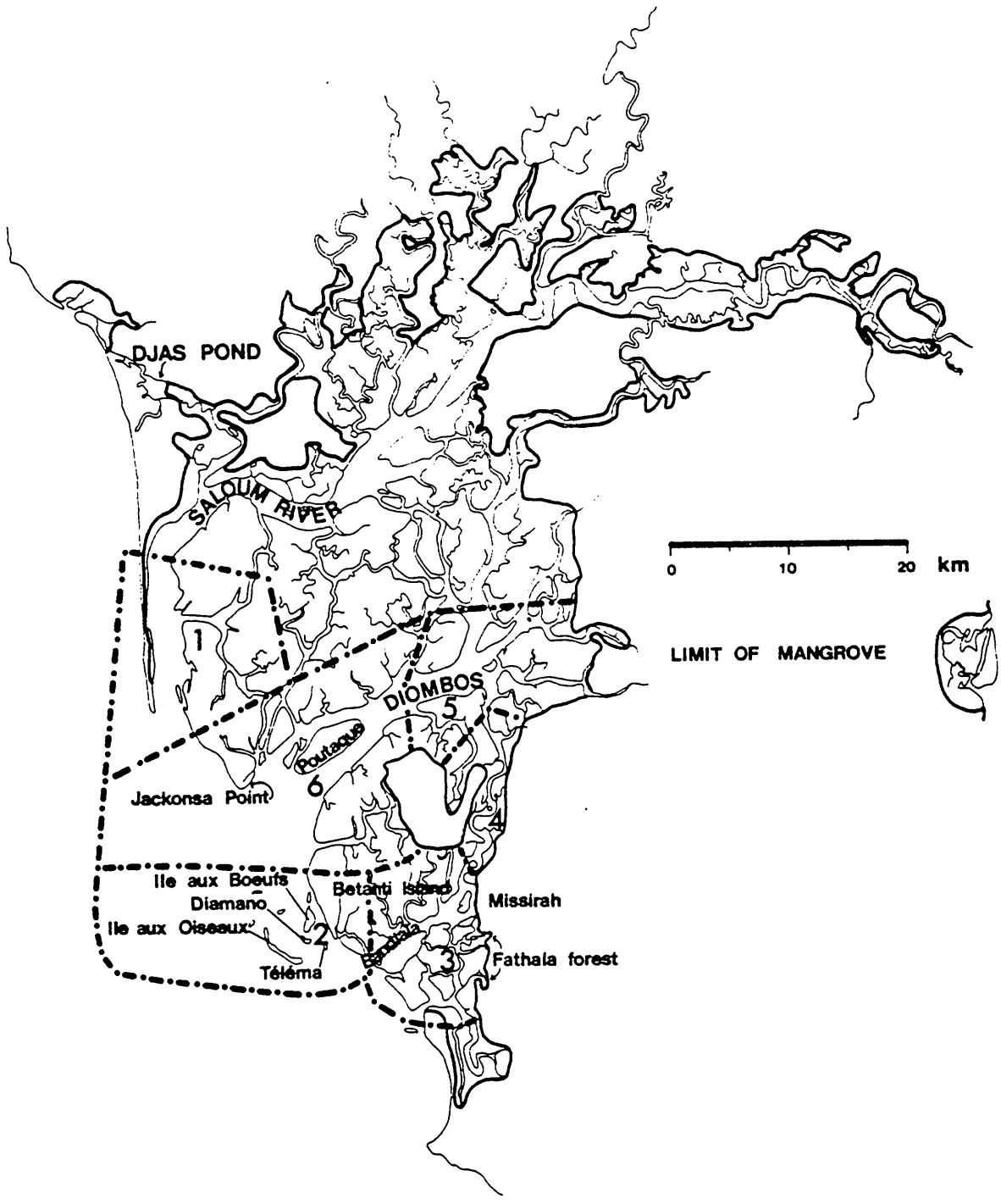

Figure 2.5 Saloum River delta.

Normally, the problem of these movements could have been removed by considering surveys either only at low or at high tides. However, there were additional constraints: mangrove forests could not be surveyed fully at low tide because some of the channels were impassable; on the other hand, since most of the Ospreys were counted at low tide along the coast or in estuaries, to have used only surveys at high tide meant discarding most of the data. As a compromise, I used surveys at low tide, but when the field data failed, Osprey numbers were estimated to be similar in the unsurveyed areas to numbers in the surveyed areas.

Most of the Ospreys counted on the thin sandspit north of the Saloum River mouth (area 1) commuted from mangroves across the river. To avoid overestimating Osprey numbers, I considered these mangroves and the sandspit as one area. Eight surveys were made: a maximum of 12 Ospreys were counted north of the river's mouth and a maximum of 22 at the river's mouth.

As many as 34 Ospreys were observed at low tide near the Saloum Islands (area 2): Ile aux Oiseaux, Diamano, Telema, and Ile aux Boeufs. All Ospreys on Ile aux Oiseaux roosted elsewhere. Observations showed that they commuted between Ile aux Oiseaux and the western part of the Betanti Island, 5 km away, or the Fathala forest, 10 km away, and this was confirmed by the re-sighting in the Fathala forest of an Osprey marked on Ile aux Oiseaux.

The Bandiala estuary between Missirah and the sea (area 3) harboured Ospreys that commuted from the mangroves in the southern

part of the Betanti Island and from the Fathala forest. Counts of 9,10,10,12 and 19 Ospreys were made at low tide in the Bandiala, while counts of 3,4,5,6,8,9 and 9 were made at other tides. Parts of the surrounding mangrove were also surveyed: 7 Ospreys were counted between a high and a low tide in the Betanti Island mangrove; 17 Ospreys were counted at high tide and 10 at low tide in half of the Fathala forest.

Counts of 2,4,5,5,8 and 8 Ospreys were made at various tides along the Bandiala between Missirah and the Diombos estuary (area 4).

Counts in the Diombos estuary (areas 5 and part of area 6) illustrate well the variation in Osprey numbers with tides. Whereas only 4 Ospreys were counted at high tide on each of two surveys in the Upper Diombos, 16 and 18 were counted at low tide. Similarly 21 and 15 Ospreys were counted at low tide on mud flats completely flooded at high tide. Area 6 also included part of the coast around Jackonsa Point where I observed 5 Ospreys at low tide.

According to Table 2.3, 130 to 170 Ospreys wintered in the areas I surveyed. These areas only covered the southern half of the Saloum River delta. In particular, the Saloum River itself was not surveyed although mangrove, interspersed with large salt flats, existed for 100 km upstream. However, to suggest that the number of Ospreys wintering in the whole delta was double the estimate for the southern half might cause an overestimate. I prefer to use a cautious total estimate of 200 to 250 Ospreys.

A maximum of 30 ospreys were observed during summer in the Saloum

	area	estimate
1	Beach north of the river mouth	10-15
1	Saloum River mouth	20-25
2	Saloum Islands including Ile aux Oiseaux	25-35
3	Lower Bandiala including the Fathala forest	30-45
4	Bandiala from Missirah to the Diombos	5-10
5	Upper Diombos	20
6	Lower Diombos including Poutaque Island	20
	TOTAL	130-170

Table 2.3. Estimates of the number of Ospreys wintering in various parts of the Saloum River delta.

area	counts
Beach north of the river mouth	0, 1, 7
Saloum River mouth	0, 0, 2, 4
Saloum Islands	0, 0, 1, 2, 2
Bandiala from Missirah to the sea	0, 0, 1, 1, 1, 1
Fathala forest (both high and low tides)	7, 8, 8, 9
Bandiala from Missirah to the Diombos	0, 0, 1, 1, 1, 1, 1, 1
Upper Diombos	1, 1, 2, 3, 6
TOTAL	8-30

Table 2.4. Ospreys counted in the Saloum River delta from mid-April to mid-August.

River delta (Table 2.4), compared with 130 to 170 estimated during winter in the area surveyed.

2.4.7 THE GAMBIA RIVER

During surveys on 25-30 January 1978, 30 Ospreys were observed along the 52 km of coast north and south of the Gambia River mouth (Table 2.5A, Figure 2.6). There was one concentration worthy of note on the Bijol Island and the nearby Solifor Point. Ospreys were also observed between Banjul and Cape St-Mary, especially near Toll Cross and Danton Bridge, but these commuted from the Kombo St-Mary mangrove and are accounted for in the survey of the Gambia River mangroves which follows.

The mangrove along the south shore of the Gambia River was surveyed up to 55 km from the river mouth and 45 Ospreys were observed (Table 2.5B, Figure 2.6). If we project this result to the unsurveyed mangrove downriver from Kerewan (431 square km: 162 square km on the south shore, including part of the Bintang Bolon, and 279 square km on the north shore), we obtain 80 additional Ospreys, or a total estimate of 125.

2.4.8 THE CASAMANCE RIVER DELTA

The 72 km of coast north and south of the Casamance River mouth were surveyed between 31 January and 6 February 1978, except for 20 km from the Presqu'Ile Aux Oiseaux to Diogue: only 6 Ospreys were seen (Figure 2.7).

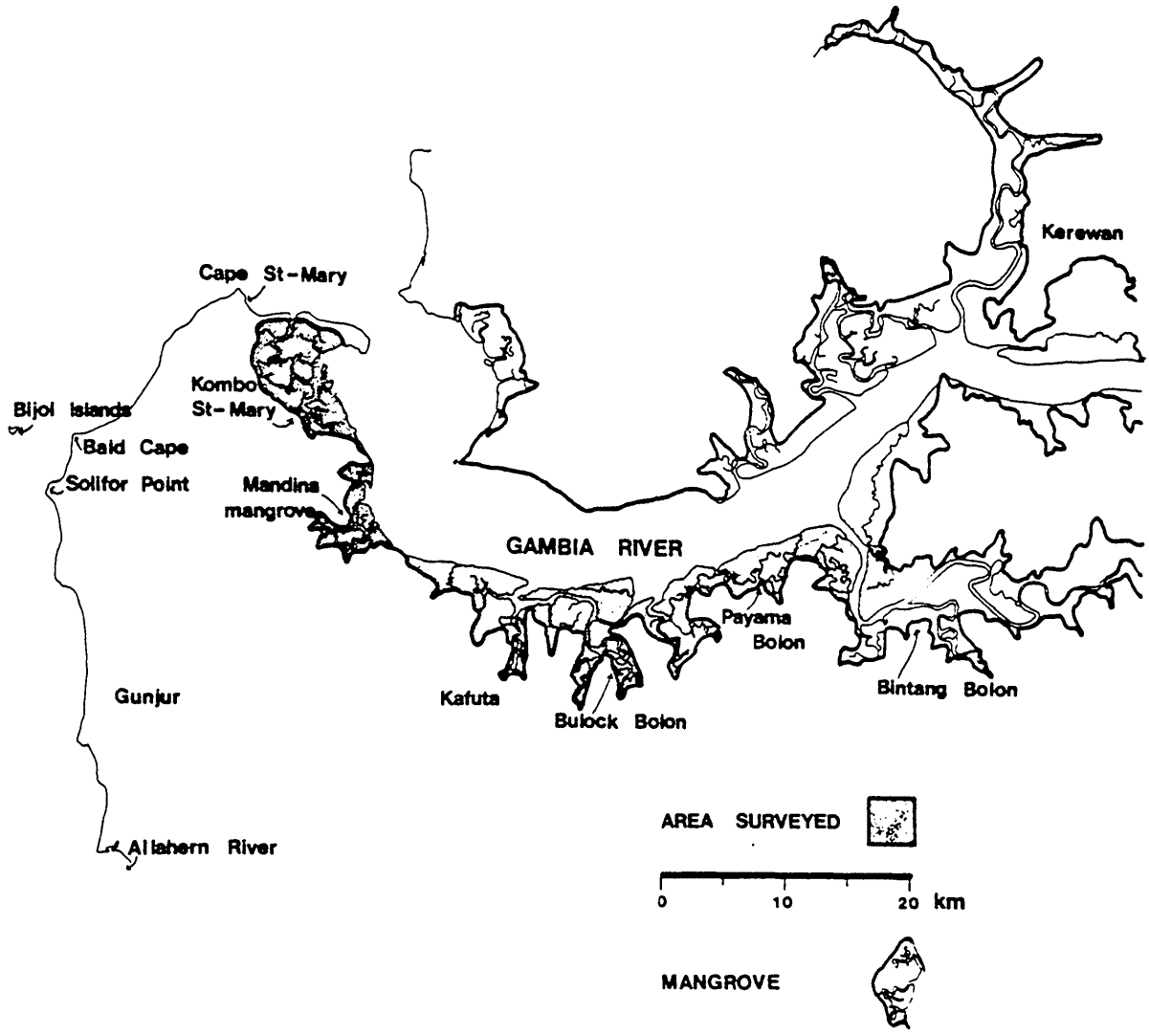

Figure 2.6 The Gambia River.

locality	number of Ospreys	distance in km
North of the river mouth	2	12
Cape St-Mary to Bald Cape	-	20
Bald Cape to Solifor Point	19	5
Solifor Point to Gunjur	4	24
Gunjur to the Allahern River	5	10

Table 2.5A. Ospreys counted north and south of the mouth of the Gambia River.

locality	number of Ospreys	area in km square
Kombo St-Mary	9	49
Mandina mangrove	11	24
Kafuta mangrove	6	40
Bulock Bolon	10	71
Payama and Bintang Bolons	9	60

Table 2.5B. Ospreys counted in parts of the mangrove along the south shore of the Gambia River.

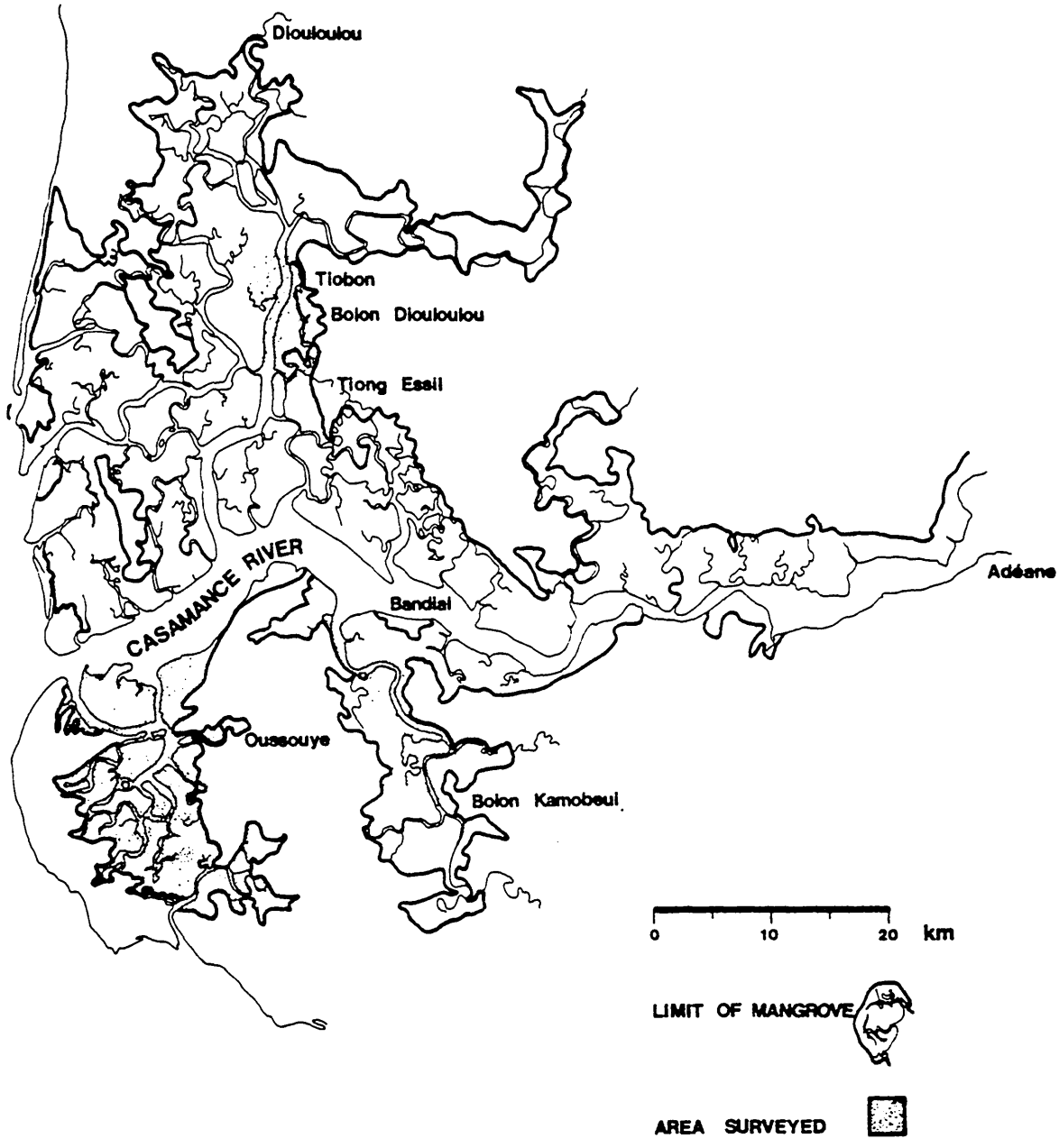

Figure 2.7 The Casamance River.

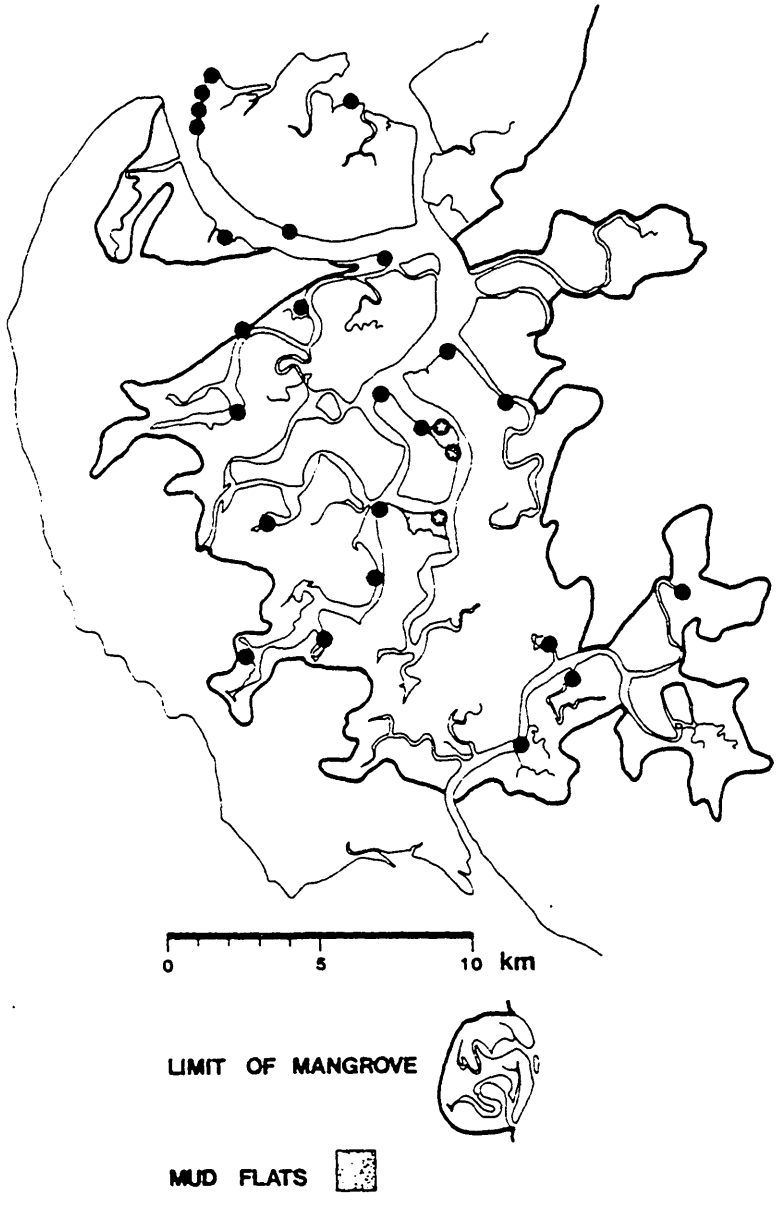

Figure 2.8. Ospreys sighted in mangrove west of Oussouye. Solid circles indicate Ospreys observed in mangrove; stars within solid circles indicate Ospreys observed on mud flats.

locality	number of Ospreys	area surveyed in square km	total area in square km	estimated population
West of Oussouye	27	198	198	27
Kamobeul Bolon	5	90	179	16
Diouloulou Bolon	8	45	805	100
Bandial to Adeane	-	-	309	37
TOTAL	40	333	1491	180

Table 2.6. Ospreys counted in mangroves of the Casamance River delta.

The Casamance River delta is a vast mangrove with a few elevated plateaux penetrating it. I decided to concentrate my efforts on the south shore, especially west of Oussouye (Figure 2.8). The mangrove to the north of the Casamance River was visited only once (Diouloulou Bolon between Tiong Essil and Tiobon), to confirm that Ospreys were present. In fact one Osprey was seen as far into the mangrove as the village of Diouloulou, 45 km from the Casamance River.

In total, 40 Ospreys were observed in 333 square km. If we project the results obtained to the unsurveyed mangrove downriver from Adeane (1158 square km, Figure 2.7), we obtain 140 additional Ospreys, or a total of 180 (Table 2.6).

2.4.9 DEPARTURE AND ARRIVAL DATES OF MIGRANTS

Osprey numbers remained stable at all sites studied from mid-October until mid-March. Departures were gradual and by the end of March Osprey numbers had decreased to less than half the winter values. However, even in mid-April, temporary concentrations were seen, suggesting that migrants from further south were passing through.

The first arrivals from Europe were observed in late August, when Ospreys reoccupied the coast between the Senegal River and the Cap-Vert peninsula where only one Osprey was seen in June, July and early August. Arrivals were spread over two months, but accelerated in late September-early October. The last to arrive were Ospreys

hatched during the summer, the earliest of which was seen on 11 October.

2.4.10 DAILY MOVEMENTS

Because of the lack of trees near foraging sites, Ospreys used the ground or low perches for feeding or resting during the day and only a few birds were found far away from foraging sites. However, at night they left the vicinity of the foraging sites to roost in trees 1 to 10 km away, where they were presumably safe from nocturnal predators such as Common Jackals, Canis aureus, and Spotted Hyenas, Crocuta crocuta. For example, at the mouth of the Saloum River, about 15 Ospreys arrived every morning within a few minutes of daybreak (Table 2.7) from their roosts in mangrove across the Saloum River; they spent the day feeding and resting at the river mouth and returned to the mangrove in late afternoon.

The proportion of Ospreys that commuted in this way varied among sites: for example, at the mouth of the Saloum River no Ospreys roosted, while at the mouth of the Senegal River some roosted in a forest of casuarina on the sandspit north of the river mouth. On the coast between the mouth of the Senegal River the Cap-Vert peninsula, where no trees were found, Ospreys left the coast in late afternoon to roost in palm groves 3-5 km inland. It was only in mangrove that Ospreys had facilities for roosting on site. However, another type of movement, related to tide, occurred there as described earlier for the Saloum River delta.

time	number of Ospreys
7:15	1
7:19	2
7:25	4
7:28	6
7:29	10
9:34	22
11:28	20
14:00	18
15:53	2
16:09	4
18:00	1
18:10	0

Table 2.7. Number of Ospreys observed at different times of the day 11 March 1979 at the mouth of the Saloum River.

2.4.11 MOVEMENTS OF MARKED BIRDS

Re-sightings of marked birds confirmed year-to-year site attachment, as found in some other migratory birds (Moreau, 1972) including raptors (Newton, 1979). Of 9 Ospreys captured in February or March 1979 at the mouth of the Senegal River, 6 were re-sighted during the winter of 1979-80. One of these did not migrate and was observed from 23 June to 16 July at the river's mouth. Another Osprey marked in October 1979, also at the mouth of the Senegal River, was found there, freshly dead, in December 1981.

Additional controls during the northern summer were made at the Djas pond; they concerned immatures, and confirmed that some Ospreys remained on their wintering grounds in their first year. Thus an Osprey captured when 8 months old in March was later seen in May, August, October and December. Another Osprey captured when 10 months old in May was seen again in August.

Data were also available on site fidelity during a single northern winter (Table 2.8). Of 25 Ospreys marked or re-sighted in September-December 1979 at the mouth of the Senegal River, 14 were seen there in February-March 1980, a surprising result given the difficulty of identifying individual Ospreys using colour rings.

Ospreys marked at the mouth of the Senegal River dispersed up to 5 km north of the river mouth and 10 km south: none were observed or reported outside this area. However, one Osprey marked near Cayar on 8 September 1979 - one of 7 marked at that site - was captured on 27 September at the mouth of the Senegal River, 100 km to the north.

months	number of Ospreys marked	Sept-Oct 1979	December 1979	Feb-March 1980
Feb-March 1979	9	1	3	5
Sept-Oct 1979	11	11	0	5
December 1979	12		12	7
Feb-March 1980	19			19
TOTAL marked or re-sighted		12	15	33

Table 2.8. Re-sightings of Ospreys marked at the mouth of the Senegal River. The last line gives the number of marked Ospreys known to have used the river mouth for each period.

month	number of Ospreys marked	March-April	May	August	October	December
January	1	0	0	0	0	0
March-April	3	3	1	1	1	1
May	2		2	1	1	1
August	1			1	0	1
October	9				9	5
December	8					8
TOTAL marked or re-sighted			3	3	11	16

Table 2.9. Re-sightings of Ospreys marked at the Djas pond in 1979. The last line gives the number of marked Ospreys known to have been at Djas pond for each of the periods.

Two other cases of movements within winter were observed: an Osprey captured in the Diombos estuary of the Saloum River delta was recaptured at the Djas pond, 30 km away, and another marked at Ile aux Oiseaux, also in the Saloum River delta, was eaten by a crocodile, Crocodylus niloticus, at Abuko in the Gambia, 50 km away (E. Brewer, pers. comm.).

Ospreys marked at sites close together in the Saloum River delta in autumm 1979 provided an opportunity to examine winter dispersal. None of the 15 Ospreys marked in October at the mouth of the Saloum River were observed in December at the Djas pond, 20 km away, nor were any of 14 Ospreys marked in early November at Ile aux Oiseaux, 40 km away. However, 5 of 9 Ospreys marked at the Djas in October were controlled there in December (Table 2.9).

Some data were obtained on the localities of origin and migratory routes of Ospreys wintering in Senegambia (Figure 2.9). Eleven Ospreys captured in Senegambia had been ringed as nestlings in Europe (Finland 5; Sweden 5; Norway 1), and nine Ospreys marked in Senegambia were later observed on migration or in the breeding grounds of northern Europe.

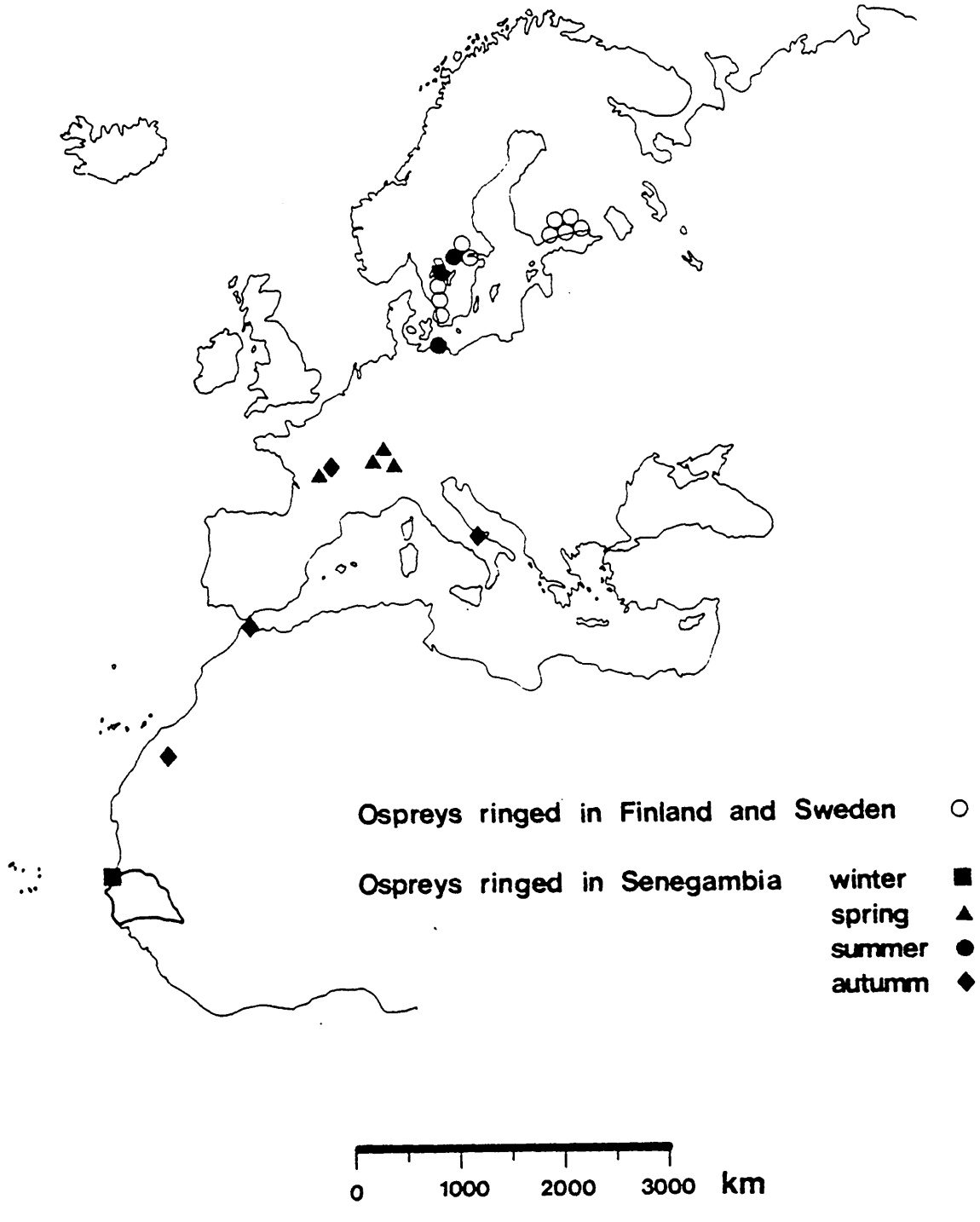

Figure 2.9 Re-sightings of Ospreys marked in Senegambia and localities of origin of ringed Ospreys captured in Senegambia.

2.5 DISCUSSION

2.5.1 POPULATION NUMBERS

Even though survey results at any one site were variable over winter, I nevertheless believe that population numbers were stable. Day to day variations in numbers resulted from daily movements between foraging and resting sites. Most surveys were done at or near foraging sites, because it was at these sites that Ospreys were most visible. But Ospreys were also found resting and feeding on perches and trees up to two kilometers inland where they could not be seen. In addition, movements to and from night roosts caused surveys in the early morning and late evening to underestimate numbers. Therefore, the highest count at any one site during winter was a minimum estimate, and this estimate held for the whole winter since few movements were observed between sites.

Observations of marked Ospreys at the mouth of the Senegal River confirmed that not all birds were counted during individual surveys. From September 1979 to December 1980, 40 Ospreys were marked; 6 birds marked in February-March 1979 were re-sighted, and another marked near Cayar was also re-sighted. Of these 47 birds, 33 were captured or re-sighted in February-early March 1980: thus between 33 and 47 marked Ospreys used the mouth of the Senegal River at that time. However, no more than half of the birds observed at the river mouth on any one day were marked. It follows that a minimum of 66 to 94 Ospreys wintered near the mouth of the Senegal River, if we

assume no movements over this period. If we compare these figures with maximum counts of 42 for the 18 km north of the river mouth and 29 for the 10 km south of the river mouth, covering a total area much greater than the river mouth vicinity, then we see that the survey figures were minimum estimates.

In the Saloum River delta there was a different problem. At high tide, Ospreys were so dispersed that only extensive surveys provided estimates of numbers, but at low tide most Ospreys left the small channels and moved to exposed mud flats along the coast, in the Bandiala and the Diombos estuaries and along the Saloum River. Therefore maximum numbers at low tide at these sites provided a minimum estimate for the surrounding area. However, these estimates excluded the Ospreys that remained in the surrounding mangrove at high tide.

Given the various estimates made above, more than 800 Ospreys wintered in Senegambia from mid-October to mid-March (Table 2.10). Population numbers may have been higher depending on the distance of penetration up the rivers. However, this penetration was limited as was shown by the near absence of Ospreys along the Gambia River 350 km inland (Dupuy and Thiollay, 1970). The majority of Ospreys were found in mangrove, fewer along coasts of sandy beaches, and fewer still in freshwater habitats.

The number of Ospreys was lower during the summer (mid-April to mid-August), but winter numbers were not reduced everywhere in the same proportion. Fewer Ospreys than expected from winter numbers

locality	estimate	distance or surface area	one Osprey per
Senegal River valley	25	148 km	5.9 km
Senegal River mouth	100	26 km	0.3 km
Senegal River to Cap-Vert	76	145 km	2.0 km
Cap-Vert peninsula	20	30 km	1.5 km
Cap-Vert to Djas pond	26	80 km	3.1 km
Djas pond	32	10 km	0.3 km
Saloum River delta coast	55-75	60 km	0.8-1.1 km
mangrove	145-175	475 km^2	2.7-3.3 km^2
Gambia coast	30	52 km	1.7 km
Gambia mangrove	125	675 km^2	5.4 km^2
Casamance coast	6	72 km	12.0 km
Casamance mangrove	180	1500 km^2	8.3 km^2
TOTAL	795-845	439 km/2650 km^2	

Table 2.10. Estimates of the number of Ospreys wintering in parts of Senegambia.

locality	summer estimate	winter estimate
Senegal River mouth	7	100
Cap-Vert peninsula to the mouth of the Senegal River	1	76
Djas pond	7	32
Saloum River delta	30	200-250
TOTAL	45	400-450

Table 2.11. Estimates of Osprey numbers in winter and summer in parts of Senegambia.

summered north of the Cap-Vert peninsula, while more than expected summered in the Saloum River delta and near the Djas pond (Table 2.11: chi-square=12.003, df=3, $p<.01$). This could result either from age-related differences in habitat during winter or from movements of immatures to preferred habitats following the departure of adults in spring. These hypotheses were not examined because of lack of data.

The number of Ospreys in Senegambia was not surprising given that over 3000 pairs breed in Europe (Osterlof, 1973; Saurola, 1976). Each pair produces on average one young every year (Odsjo and Sondell, 1976; Saurola, 1976), and delayed maturity means a large immature age class. It then follows that more than 10,000 Ospreys winter in West Africa (the area where rings have been recovered), along the coast from Mauritania to Gabon (6000 km), and inland along the major rivers. The number of Ospreys estimated in Senegambia was as expected from the length of its coast (450 km) and the importance of its rivers.

2.5.2 DISPERSION

The mode of dispersion was related to habitat. Large groupings of over 20 birds were found at the mouths of the Senegal and Saloum Rivers and to a lesser extent at the Djas pond. There were few signs that birds avoided each other at these sites. On the contrary, Ospreys often perched within touching distance of each other and, as an extreme example, five birds were observed perched

together on a beached tree trunk 5 m long.

Dispersion seemed random along coasts of sandy beaches between river mouths, and I could test this for three surveys of the coast between Fass Boue and Yoff, where distances between birds varied from a few meters to a few kilometers. This was done by comparing the frequency distribution of distances between Ospreys with a Poisson distribution. Dispersion was random in two surveys (chi-square=4.56 and chi-square=6.66, df=4, $p<.05$) and became random in the third survey if we excluded from the analysis Ospreys concentrated at the shell mound north of Cayar. The pattern was not related to the distribution of feeding and resting perches along the coast as there were many more perches than birds.

In contrast, in closed mangrove Ospreys were regularly spaced 1.5-3 km apart (Figure 2.7, chi-square=8.97, df=3, $p<.05$) and were rarely in sight of each other. These Ospreys were usually perched 5 to 10 m high in mangrove trees at the waters edge from which they could hunt. Although no aggressive behaviour was observed the regular spacing suggests that dispersion was socially determined. To an Osprey hunting from a channelside perch, spacing probably stopped other Ospreys from disturbing the area visible from the perch and interfering with hunting. Interestingly, these same Ospreys sometimes aggregated at low tide when on muflats where perches were too near the ground or too far from water to permit hunting.

2.5.3 POPULATION DENSITY

When discussing variations in population density it is necessary to separate (1) temporary concentrations due to Ospreys over a wide area going to favourable sites to feed or rest, from (2) variations in population density between areas. Concentrations on mud flats in open mangrove at low tide are an example of the first case. They arose from the limited supply of open water for hunting in the surrounding closed mangrove, and of suitable perches for feeding and resting in the open mangrove. However, in the second case, Ospreys were disproportionately abundant in some areas such as at the mouth of the Senegal River, irrespective of perching prospects.

Along the coast, changes in population density did not appear to be caused by social behaviour, but were more likely related to food, better areas attracting more birds, less attractive areas retaining birds unaware that better areas existed. This will be discussed in Chapter 3, and it is sufficient to mention here that the most important concentrations were at river mouths where fish were more abundant than along coasts of sandy beaches.

In mangrove, social behaviour probably reduced the density of Ospreys, but I have no data to show this. Here again, differences in density between mangrove areas could be related to food abundance, but in this case through the action of social behaviour (Newton, 1979).

2.5.4 FISH EAGLES

Another factor that could have affected Osprey distribution was the presence of Fish Eagles, Haliaeetus vocifer. In Senegambia, Ospreys and Fish Eagles preferred different habitats (Table 2.12). Fish Eagles were rare along the coast but abundant elsewhere, especially in the Senegal River valley. Fish Eagles did not hunt much on the wing and were most numerous along rivers or around lakes with hunting perches overlooking the water, as at Lake Victoria in Uganda (Eltringham, 1975). In contrast, Ospreys hunted on the wing and were numerous in open habitats along the coast with no hunting perches.

Although both species were numerous in mangrove, only two aggressive encounters were observed: on one occasion a Fish Eagle unsuccessfully tried to rob an Osprey of its fish while on the other an Osprey drove away a Fish Eagle in flight by repeatedly diving at it.

In the case of Fish Eagles and Ospreys one cannot talk of interspecific territoriality, because the behaviour of both species depended on whether the Osprey had eaten or not: whereas Ospreys seemed to avoid hunting in sight of a Fish Eagle, presumably because the Fish Eagle might have tried to steal the fish (Brown, 1980), they frequently perched near eagles after having fed, on occasion as little as 50 m away. At no time did Fish Eagles avoid Ospreys. Fish Eagles tended to be localized in mangrove, often in pairs, leaving free to Ospreys most of the closed mangrove and any open

habitat	Ospreys	Fish Eagles	Ospreys/ Fish Eagles
Coast	280	11	26:1
Mangrove	166	26	6:1
Senegal River Valley	12	38	1:3
TOTAL	458	75	

Table 2.12. Number of Ospreys and Fish Eagles observed in three habitats of Senegambia in the winter of 1978.

mangrove or coastal beaches. The avoidance by Ospreys of hunting in sight of a Fish Eagle, probably slightly decreased the number of Ospreys in mangrove, and together with the spacing of Ospreys themselves limited the number of Ospreys in mangrove.

In freshwater habitats, Fish Eagles might have excluded Ospreys, but I have too little data to check this. However, along the coast the two species appeared to be distributed independently of each other.

2.5.5 MALE-FEMALE PAIRS

In a few cases, two Ospreys were regularly seen together at sites along the coast. Although these birds were not sexed, frequently one was large with a dark breast band and the other smaller with a light breast band, suggesting that they were male-female pairs. In the intention of stimulating a pair to breed, I put up four nesting platforms at the mouth of the Senegal River in 1979 and topped them with artificial nests. One pair frequented one of these nests throughout February 1980 (Figure 2.10), but courtship displays or courtship feeding were not observed.

Figure 2.10 Pair of Ospreys at an artificial nest site at the mouth of the Senegal River.

CHAPTER 3

FOOD AND FORAGING OF OSPREYS IN SENEGAMBIA

3.1 INTRODUCTION

Whereas the diet and foraging behaviour of Western Palearctic Ospreys on their breeding grounds has been documented by many authors (Schnurre, 1961; Moll, 1962; Nordbakke, 1974; Green, 1977; Hakkinen, 1978), their food and foraging behaviour in the wintering grounds of West Africa is wholly unknown, except that the diet consists of fish. The purpose of this chapter is to describe the food and foraging behaviour of Ospreys in the range of habitats found in Senegambia, from open seashore to closed mangrove, with emphasis on diet composition, prey size and foraging efficiency. The study area was described in detail in the preceding chapter.

3.2 STUDY AREA

Food and foraging behaviour were studied at 8 sites representing different habitats:

Coastal sand dune: two localities between the mouth of the Senegal River and the Cap-Vert peninsula (1) 15 km north of Cayar and (2) 9 km south of Cayar.

Rocky shore: two localities on the Cap-Vert peninsula, (1) the Ouakam-Ngor-Yoff coast north of the peninsula, and (2) Ile de la Madeleine, a rocky island 2 km offshore.

River mouth: two localities, (1) on the Langue de Barbarie at the mouth of the Senegal River between St-Louis and Tare, a sand spit bordered by the open sea on one side and the Senegal River on the other, and (2) at the Pointe de Sangomar at the mouth of the Saloum River, a sand spit with open sea on one side, breakers and shallow waters at the tip, and areas of calm water on the river side.

Shallow coastal tidewaters and ponds connected to the sea: two localities on salt flats north and south of the Djas pond, between Joal and Palmarin.

Inshore islands: at Ile aux Oiseaux and surrounding islands at the mouth of the Saloum River, a series of small vegetated sand bars 3 km away from the mainland.

Open mangrove: at the Diombos, an intrusion of the sea into the mangrove of the Saloum River delta, 15 km deep and 3-4 km wide, consisting of shallow mudflats, some exposed at low tide, and cut by deep channels.

From it radiate numerous channels that drain the surrounding mangrove.

Closed mangrove: three localities in the Saloum River delta along channels, 100-200 meters wide, cutting the mangrove.

3.3 METHODS

3.3.1 DIET

When an Osprey feeds, it tears the flesh off the fish from the head downward to the tail. Only small and easily broken bones are ingested, so that pellets are not useful in the study of food; however, guts, eyes, large bones and tails, from all except some small fish, are dropped under feeding perches. I used such remnants to assess the diet.

The results were biased, because remains of different fish species varied according to their (1) conspicuousness to the collector, (2) durability when exposed to the elements, and (3) probability of the Osprey eating or breaking them beyond recognition. In addition, remains were often covered by sand or blown away, and at most sites scavengers such as Grey Herons, *Ardea cinerea*, turnstones, *Arenaria interpres*, gulls, *Larus fuscus* and *L. cirrocephalus*, Common Jackals, *Canis aureus*, and Ghost Crabs, *Ocypoda cursor*, quickly removed fish remains. For these reasons, more than 150 wire mesh baskets (Figure

Figure 3.1 Wire mesh basket for collecting fish remains (Photo Yves Prevost).

3.1) were installed under favourite feeding perches at the different sites, to catch remains. These perches were then visited and the remains collected on a more or less regular basis. Whenever necessary, natural perches unsuitable for installing baskets were removed and replaced by suitable artificial perches. Baskets in mangrove were set on artificial perches planted in shallow water or on mud flats flooded at high tide.

At the Djas pond, Ospreys fed on hard salt flats where scavengers were rarely seen and where each year floods during the rainy season (June-October) destroyed remains. Remains were collected off the ground from December 1977 until May 1979, after which baskets were installed to permit collection during the rainy season. Baskets were not used for the rocky shore of the Cap-Vert peninsula, so diet data were patchy and came from only a few visits, when remains were collected at the base of feeding perches or from cliffs.

Items discarded by Ospreys included: hard bones from the head, the opercula being the commonest; the uneaten portion of the tail; wings (pectoral fins) from flying fish, Cheilopogon spp.; bills from garfish, Strongylura spp.; the longest anal fin ray from grunts, Pomadasys spp.; entire skulls from catfish, Arius spp..

Fish were not eaten on the wing by Ospreys and all food items, even the smallest, were taken to feeding perches. The opercula of even the smallest fish were removed by Ospreys before the fish was eaten and the basket mesh was small enough to keep all opercula from falling through. Thus baskets provided a representative sample of

Opercula	hard opercula	Mugilidae
		Ethmalosa dorsalis
		Sardinella spp.
		Pomadasydae
		Serranidae
		Cichlidae
		Sparidae
		Ariidae
		Smaris melaneurus
		Abudefduf spp.
	soft opercula	most Carangidae
		Galeoides decadactylus
		Sciaenidae
		Albula vulpes
		Elops spp.
	very soft opercula	Exocoetidae
		Belonidae
		Thunnidae and related families
		Sphyraena spp.
		Ilisha africana
		Chloroscombrus chryusurus

(continued on the next page)

Table 3.1. Remains of fish taken by Ospreys found at feeding perches in Senegambia. Tails of larger fish were more likely to be found than tails of smaller fish. In In particular few Sardinella spp. tails were found.

Tails	tails likely to be intact	Exocoetidae Pomadasydae Serranidae Carangidae Ariidae Belonidae Thunnidae and related families *Galeoides decadactylus*
	tails likely to be broken	Mugilidae Clupeidae including *Ethmalosa* *Sardinella* *Ilisha* Cichlidae Sciaenidae *Sphyraena* spp. *Albula vulpes* *Elops* spp. *Smaris melaneurus* *Abudefduf* spp.
Others	pectoral fins	Exocoetidae
	bills	Belonidae
	anal fins	Pomadasydae

Table 3.1. (contd.)

the diet at the sites where they were used.

For identifications, I boiled bony parts and brushed them clean of flesh. Identifications were made by comparing remains with equivalent fish parts in a reference collection made for the study. Fish in the reference collection were determined from the key of Blache *et al*. (1970). A revised nomenclature and key (Thomson, pers. comm.) were used for mullet, *Mugil* spp. and *Liza* spp., family Mugilidae. The nomenclature of Hureau and Monod (1973) is followed where it differs from Blache *et al*.

Species could be grouped according to the likelihood of finding remains intact (Table 3.1). Opercula were used to determine prey size and both these and other remains were used to assess diet: the true diet lies somewhere between the diets as assessed by these two methods. Fortunately, species with the softest opercula, the ones least likely to be found, had some of the hardest alternative remains.

3.3.2 PREY SIZE

Weight and length for 13 fish species were estimated from opercula collected in the field, using linear regressions established between opercula length, fish weight and fish length in reference samples collected from near Osprey foraging sites (Table 3.2). I used the opercula measure which gave the best correlation with fish weight and length in the reference sample. Because of different opercula shapes and break patterns, the measured characteristic varied from

species	length		weight	
	a	b	A	B
Liza dumerilii	1.243	-8.771	3.283	-5.337
Liza grandisquammis	1.000	26.717	3.039	-4.869
Liza falcipinnis	1.295	-8.718	3.360	-5.509
Mugil curema	1.108	-14.200	3.231	-5.323
Mugil cephalus	1.088	-13.705	3.315	-5.628
Mugil bananensis	0.966	9.748	3.249	-5.426
Ethmalosa dorsalis	1.057	-37.800	3.523	-6.116
Sardinella aurita	0.933	53.015	2.632	-3.723
Sardinella maderensis	1.045	24.865	3.209	-5.029
Dicentrarchus punctatus	1.310	-17.560	3.239	-5.216
Pomadasys jubelini	0.852	8.350	2.676	-4.136
Sarotherodon melanotheron	0.796	1.396	2.840	-4.625
Smaris melaneurus	0.830	128.295	2.823	-4.340

Table 3.2. Linear regression parameters between opercula (mm) and fish length (cm), and opercula and fish weight (kg) for reference samples of 13 fish species eaten by Ospreys in Senegambia.

$$\text{estimated length} = a \times \text{oper} + b$$
$$\log(\text{estimated weight}) = A \times \log(\text{oper}) + B$$

where oper is the length of the opercula collected in the field.

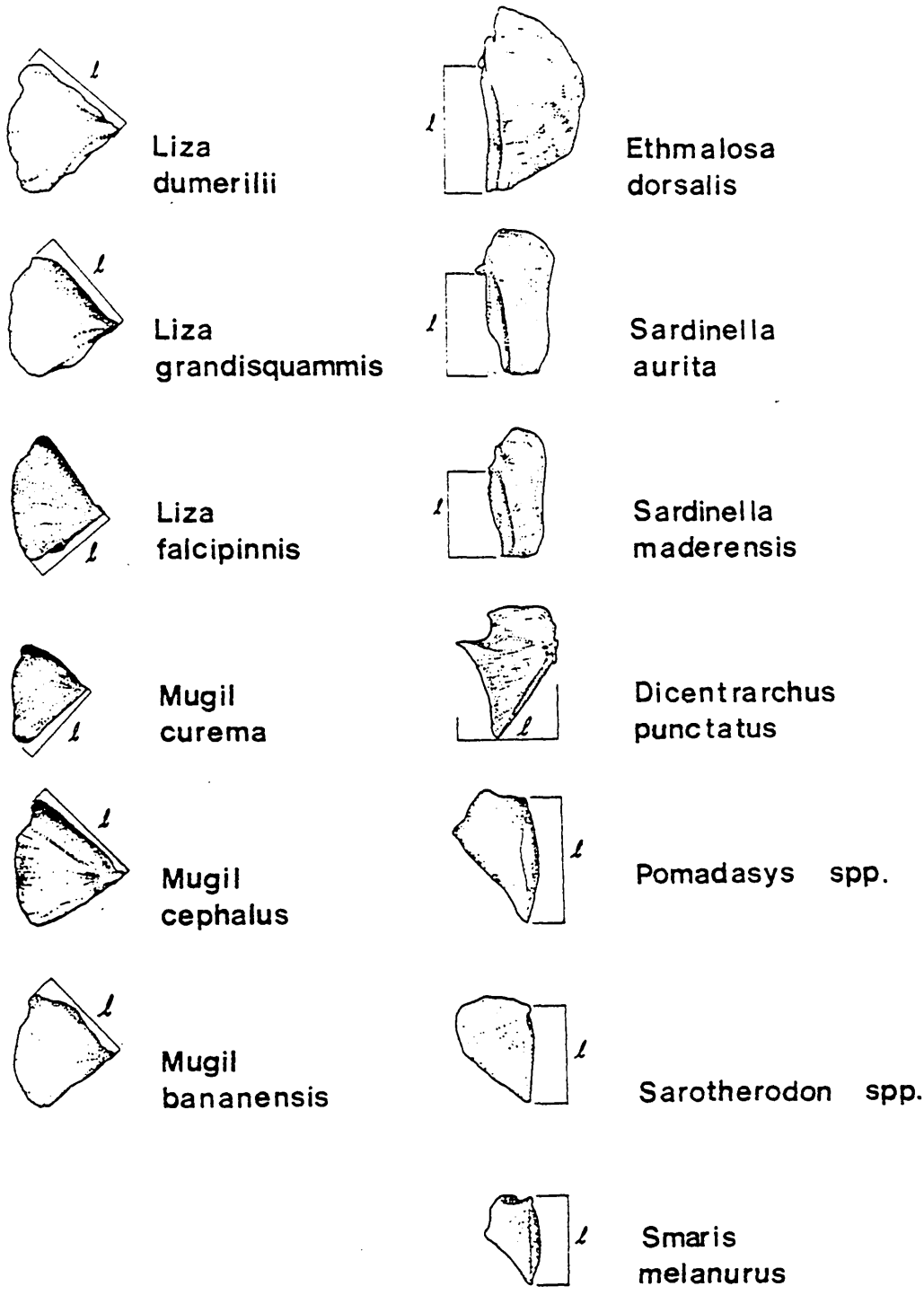

Figure 3.2 Opercula of fish taken by Ospreys in Senegambia.

species to species (Figure 3.2). For Clupeidae, sardines, Sardinella spp., and Fimbriated Herring, Ethmalosa dorsalis, I used the forward edge below the articulation with the hyomandibular bone; for mullet, I used the forward edge either above or below the articulation, depending on the species, but included the articulation; for the other species I measured the forward edge below the articulation and included part of the articulation. The regression coefficients for Pomadasys jubelini were also used for the less common P. peroteti and P. rogeri: differences between species were assumed to be small. The opercula shapes of tilapia, Sarotherodon melanotheron, S. nilotica and S. galilea, were too variable to separate the species. I used the regression coefficients of S. melanotheron for all three species, although these slightly underestimated the weight and length of the other two species. Otherwise, all intact opercula could be assigned to species, including sibling species of mullet. Mullet opercula damaged beyond specific recognition were put down as `mullet unspecified'.

The average weight of two important fish species, flying fish and garfish, could not be properly estimated from opercula. Flying fish were large and of uniform size at 250-450 grams (average 400 grams), while garfish were more variable at 150-400 grams (average 250 grams). All other important species had hard opercula, and weight estimates were obtained. The less important species that I found were usually restricted to one season and one location.

3.3.3 FORAGING

Observations of foraging were made to compare the hunting success and energetics of Ospreys in different habitats. Data were collected at 5 sites from 1977 to 1980: coastal sand dunes (14 days), the mouth of the Senegal River (88 days), the mouth of the Saloum River (17 days), shallow coastal tidewaters near the Djas pond (18 days) and inshore islands (26 days). Other observations made in mangrove are grouped. Periods of observation varied from 1 to 10 consecutive hours and ranged from sunrise to sunset. Observations were made with binoculars and a 15-45X telescope.

Hunting Ospreys were recognizable by their behaviour in flight, with frequent stops in mid-air, so that Ospreys not hunting could be readily excluded. During each hunt I recorded the Osprey's movements, its height above the water, and the timing and success of each plunge into the water. Hunting success was assessed in two ways:

(1) Dive success: the proportion of dives that were successful. Dives where the Osprey did not touch the water and intention movements were excluded from calculations of dive success since they did not represent completed attempts to catch a fish.

(2) Time per capture: the ratio of all hunting time observed, including hunting time followed by quitting, to

the number of successful dives. Each Osprey was included from the time it first came into view until it was either lost to view, caught a fish or quit.

Ospreys often stopped hunting, rested shortly and then resumed hunting. To take into account only the hunting time immediately prior to a capture would have seriously underestimated the time spent hunting to catch a fish. This is why I decided to include hunting time followed by quitting in the calculation of time per capture. One drawback of this method was that all hunting bouts leading to a capture had to be observed and recognized as coming from the same bird before I could determine the time required to catch a fish by an individual Osprey. As this was very rarely possible, observations could not be put into statistically comparable units. In particular, standard deviations could not be calculated for times per capture.

3.4 RESULTS

3.4.1 THE DIET AT EACH STUDY SITE

3.4.1.1 Coastal sand dunes

In December and January, flying fish and garfish were the main prey, and the average weight of individual fish well exceeded 300 grams, while in February and March, very large grunts were the main prey and average weight exceeded 400 grams. The diet during the rainy season, from July to September, was again different: small sardines predominated, together with various jackfish (Carangidae); average weight of prey was only 176 grams.

3.4.1.2 Rocky shores

The diet was more varied than elsewhere. The main prey were small fish of 100 to 200 grams, *Smaris melanurus* and *Abudefduf* spp., inhabiting rocky shores, but pelagic species such as flying fish and sardines were also taken.

3.4.1.3 The mouth of the Senegal River

Mugil cephalus made up the majority of catches all year round; the second most important species, Fimbriated Herring, at no time comprised more than 10-15% of the diet. Flying fish were important seasonally in December and January, making up nearly all catches by Ospreys on certain days.

When the river was in flood, from August to November, small

period	weights in grams			number of opercula
	0-200	200-400	>400	
April to July	76	14	10	42
August to mid-October	49	48	3	69
mid-October to mid-December	57	33	10	60
mid-December to January	31	40	29	156
February to March	39	35	25	167

Table 3.3. Weight distribution (%) of Yellow Mullet, Mugil cephalus, caught by Ospreys at the mouth of the Senegal River between April 1979 and March 1980. Estimated from opercula.

mullet, Mugil cephalus and Liza dumerilii, concentrated in a pocket of clear freshwater, in a cul-de-sac south of the river mouth. Ospreys hunted mostly there rather than at sea which was then brown with silt.

Large Mugil cephalus weighing more than 500 grams migrated between the Senegal River and Mauritania, as reflected in fishing catches in St-Louis (Centre de Recherche Oceanographique de Dakar Thiaroye, unpub.), 18 km north of the river mouth. They came with the Canarian waters in late November, and stayed until March-April, when the warm Guinean waters moved back up the coast. The weight distribution of Mugil cephalus (Table 3.3) captured by Ospreys reflected the change in absolute density. When these were present, most captures were made at the river outlet, rarely out to sea where mostly flying fish were captured.

3.4.1.4 The mouth of the Saloum River

Fimbriated Herring formed the major prey most of the year, but in October-December Liza dumerilii predominated. Mugil cephalus, M. curema and M. bananensis were less important.

3.4.1.5 Shallow coastal tidewaters

Food was from two locations, Djas north and Djas south, only 2 km apart, with no obvious habitat differences. The diets were expected to be identical at the two sites, but in fact differed in some respects. Three distinct prey seasons could be recognized which

took into account local factors but which did not exactly match recognized seasons on land: September-December, January-April and May-August.

In September, the rains made water levels rise in the Djas pond and mullet invaded it. They stayed until January, as shown by the activities of local fishermen, but then returned to sea as water levels dropped in the pond. During this period, September to December, Ospreys foraged in the pond and at sea, two sites a few hundred meters apart, each with its own fish species. Mugil cephalus was the main fish taken at both sites, but while it was the heaviest at Djas south, on average over 300 grams, it was among the lightest at Djas north, especially in December when it averaged well under 200 grams.

In January-April, Liza falcipinnis was the main prey and was also the heaviest, exceeding 300 grams on average; however, other mullet, such as Mugil bananensis with an average weight less than 200 grams, and Fimbriated Herring formed an important part of the diet especially at Djas south. Most fish, including all Liza falcipinnis and Fimbriated Herring, were taken at sea, but other mullet were still taken in the Djas pond. Flying fish were important in January-February, making up almost all catches on certain days. At Djas south, Ospreys abruptly shifted in May to a diet almost exclusively of Fimbriated Herring, but the shift was not as pronounced at Djas north, where Liza falcipinnis remained important.

3.4.1.6 Inshore islands

Mugil bananensis, Liza grandisquammis and Fimbriated Herring were the main prey; catfish and tilapia were less important. Remains of larger mullet, such as Mugil cephalus or Liza falcipinnis were never found. The average prey weight was low and, of the three main prey species, only Fimbriated Herring was consistently over 200 grams.

3.4.1.7 Open and closed mangrove

Mugil bananensis and small Fimbriated Herring were the main prey in open mangrove; Mugil bananensis and tilapia were the main prey in closed mangrove. The average weight of prey was less than 200 grams at both sites, with no remains of fish over 400 grams ever collected in open mangrove and none over 250 grams in closed mangrove.

3.4.2 DIET COMPOSITION

Although the diet was varied (54 identified species are listed in Table 3.4), the bulk, except along coastal sand dunes north of the Cap-Vert peninsula and around the Cap-Vert peninsula itself, was made up of Fimbriated Herring and six species of mullet, Mugil cephalus, M. bananensis, M. curema, Liza falcipinnis, L. dumerilii and L. grandisquammis (Table 3.5). These were all bottom feeding, shoaling fish characteristic of shallow coastal waters. One or two of these fish dominated the diet at each site, but the list of species and their relative importance differed between sites. Along coastal sand dunes between the mouth of the Senegal River and the

family	species	english name
Carcharhinidae		
Elopidae	*Elops lacerta*	
Albulidae	*Albula vulpes*	
Clupeidae	*Ilisha africana*	
Clupeidae	*Ethmalosa dorsalis*	Fimbriated Herring
Clupeidae	*Sardinella aurita*	sardine
Clupeidae	*Sardinella maderensis*	sardine
Tetraodontidae	*Ephippion guttifer*	
Tetraodontidae	*Lagocephalus lagocephalus*	
Tetraodontidae	*Lagocephalus laevigatus*	
Belonidae	*Strongylura crocodila*	garfish
Hemirhamphidae		
Exocoetidae	*Cheilopogon heterurus*	flying fish
Fistularidae	*Fistularia serrata*	
Sphyraenidae	*Sphyraena* spp.	barracuda
Mugilidae	*Mugil curema*	
Mugilidae	*Mugil cappurrii*	
Mugilidae	*Mugil cephalus*	Yellow Mullet
Mugilidae	*Mugil bananensis*	mullet
Mugilidae	*Liza falcipinnis*	mullet
Mugilidae	*Liza grandisquammis*	mullet
Mugilidae	*Liza dumerilii*	mullet
Polynemidae	*Galeoides decadactylus*	plexiglass nose
Serranidae	*Cephalopholis taeniops*	
Serranidae	*Epinephelus* spp.	grouper
Serranidae	*Dicentrarchus punctatus*	sea bass
Pomadasydae	*Pomadasys jubelini*	grunt
Pomadasydae	*Pomadasys rogeri*	grunt
Pomadasydae	*Pomadasys peroteti*	grunt
Pomadasydae	*Diagramma mediterraneus*	
Pomadasydae	*Plectorhynchus macrolepsis*	
Pomadasydae	*Parapristipoma* spp.	
Sciaenidae	*Pseudotolithus* spp.	
Carangidae	*Trachurus* spp.	
Carangidae	*Caranx rhonchus*	jackfish
Carangidae	*Caranx senegalus*	jackfish
Carangidae	*Lichia glauca*	
Carangidae	*Chloroscombrus chryusurus*	
Carangidae	*Trachinotus maxillosus*	
Carangidae	*Vomer setapinnis*	

(continued on next page)

Table 3.4. Scientific names and families of fish taken by Ospreys in Senegambia.

family	species	english name
Pomatomidae	Pomatomus saltatrix	
Sparidae		
Maenidae	Smaris melanurus	
Monodactylidae	Psettus sebae	
Pomacentridae	Abudefduf spp.	
Acanthuridae	Acanthurus monroviae	
Balistidae	Balistes capriscus	
Monocanthidae	Stephanolepsis hispidus	
Thunnidae		tuna
Trichiuridae	Trichiurus lepturus	
Cichlidae	Sarotherodon melanotheron	tilapia
Cichlidae	Sarotherodon galileus	tilapia
Cichlidae	Sarotherodon niloticus	tilapia
Ariidae	Arius spp.	catfish

Table 3.4. (contd.)

site	January-May			June-December		
	Mullet (%)	Fim. Her. (%)	number of opercula	Mullet (%)	Fim. Her. (%)	number of opercula
Coastal sand dune	51	7	(45)	20	0	(56)
Rocky shore	5	0	(159)	0	0	(14)
Mouth of the Senegal River	85	6	(662)	81	6	(210)
Mouth of the Saloum River	57	37	(601)	72	24	(247)
Shallow coastal tidewaters	60	29	(3022)	66	29	(650)
Inshore islands	77	15	(146)	37	55	(62)
Open mangrove	89	11	(36)	83	16	(64)
Closed mangrove	100	0	(14)	17	0	(12)

Table 3.5. Comparison between sites of the percent importance of mullet and Fimbriated Herring in the diet of Ospreys in in Senegambia.
The mullet group consists of: Mugil cephalus
Mugil curema
Mugil bananensis
Liza falcipinnis
Liza dumerilii
Liza grandisquammis
Fim. Her. is Fimbriated Herring, Ethmalosa dorsalis.
Diet determinations were made from opercula collected under feeding perches and confirmed by tails also collected in the same manner. Flying fish, Cheilopogon heterurus are not taken into account on individual days from December to February.

site	year	December (%)	January (%)	February -March (%)	number of tails
Coastal sand dunes	1979	29	no data	0	(92)
Senegal River mouth	1978-79	no data	no data	8	(52)
	1979-80	16	40	1	(186)
Shallow coastal tidewaters	1977-78	36	41	49	(458)
	1978-79	23	20	7	(904)
	1979-80	0	no data	no data	(66)

Table 3.6. Relative importance (%) of flying fish, Cheilopogon heterurus, in the diet of Ospreys in Senegambia, as determined from fish tails in prey remains collected under feeding perches. No flying fish remains were found before December or after March.

Cap-Vert peninsula, associated with the absence of shallow waters, Ospreys fed on more pelagic species while around the Cap-Vert peninsula the diet reflected the rocky shore.

Apart from these two sites, species other than mullet or Fimbriated Herring were only seasonally important: in particular flying fish made up nearly all catches on certain days in December-March (Table 3.6). Flying fish moved down the coast of Senegambia with the Canarian waters in early December and stayed until March. Although they were usually found a few kilometers offshore, too far for Ospreys, they drifted close to shore in rough weather because of westerly winds, and were then caught by Ospreys. Few flying fish were caught in the Saloum River delta where waters were shallow and sites were protected from the open sea by offshore sand bars; evidently none were caught in the mangrove. Ospreys also caught them (but 3 km out at sea or more) along the coast south of the Gambia River.

3.4.3 PREY SIZE

The average weight of fish caught by Ospreys varied with the season and often differed between nearby sites. The average weight of most prey species was between 200 and 300 grams, but the range of weights for individual items was very wide, from 42 to 1017 grams. Some of the species were on average much heavier than others, but individuals of only four species exceeded 700 grams, all during winter (Table 3.7). Average weight of fish was highest at sites

site	Liza dum.	Liza falc.	Mugil ceph.	Pomadasys	large fish (total all fish)
Coastal sand dunes	0	0	3	6	9 (89)
Mouth of the Senegal river	0	2	14	1	17 (778)
Mouth of the Saloum river	0	0	4	0	4 (730)
Shallow coastal tidewaters	0	3	2	3	8(2648)
Inshore islands	1	0	0	0	1 (159)

Table 3.7. Number of fish with an estimated weight over 700 g caught by Ospreys in Senegambia. Species are Liza dumerilii, Liza falcipinnis, Mugil cephalus and Pomadasys spp.

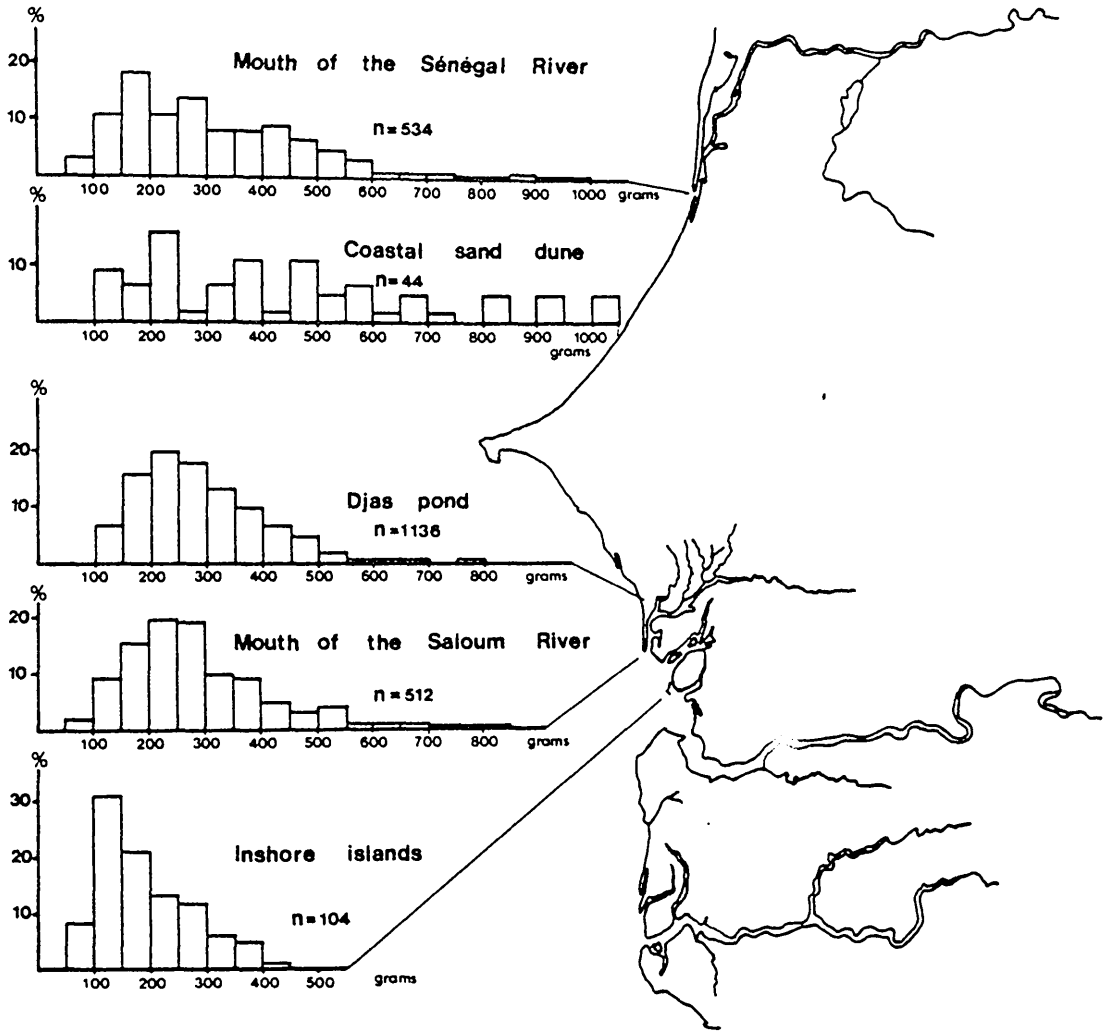

Figure 3.3A Weight distribution of fish caught by Ospreys in Senegambia in September-December.

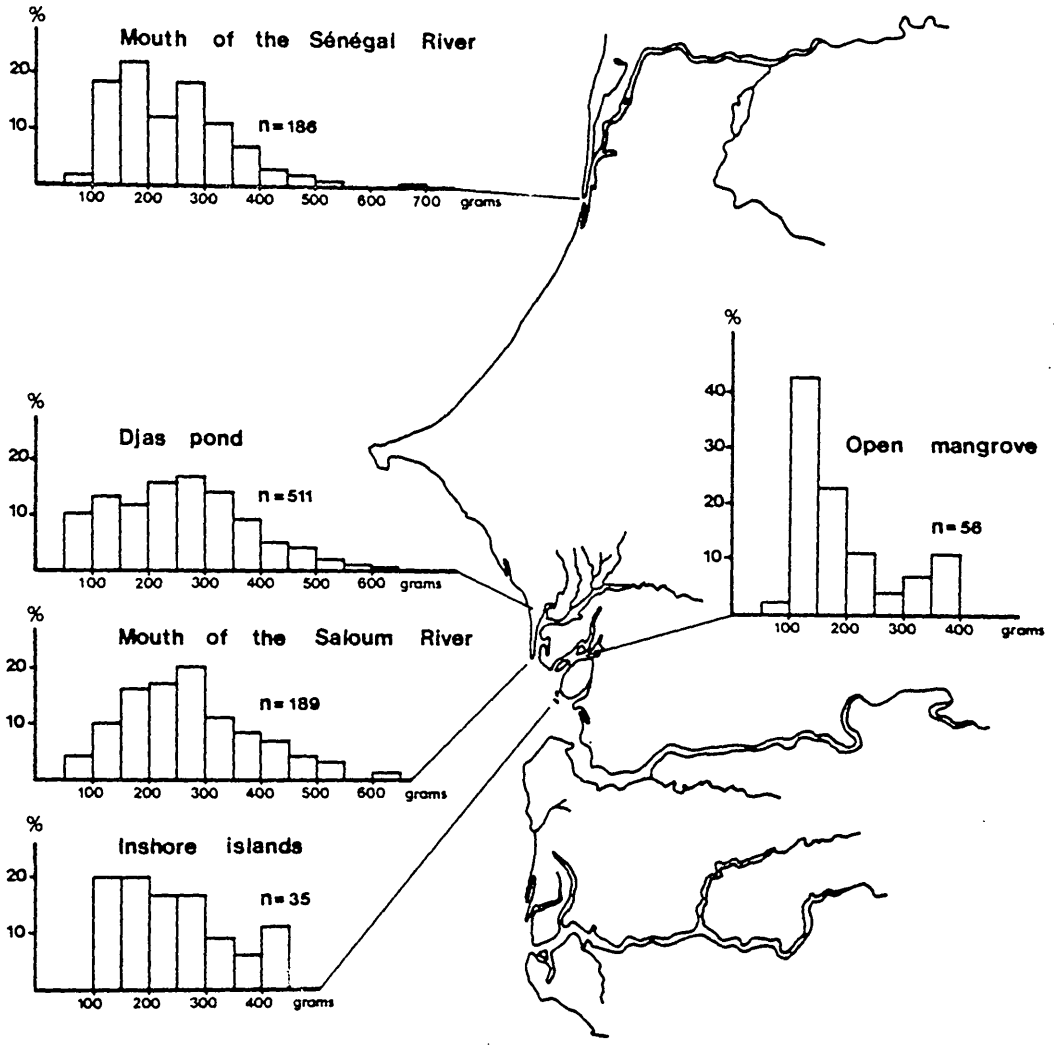

Figure 3.3B Weight distribution of fish caught by Ospreys in Senegambia in January-March.

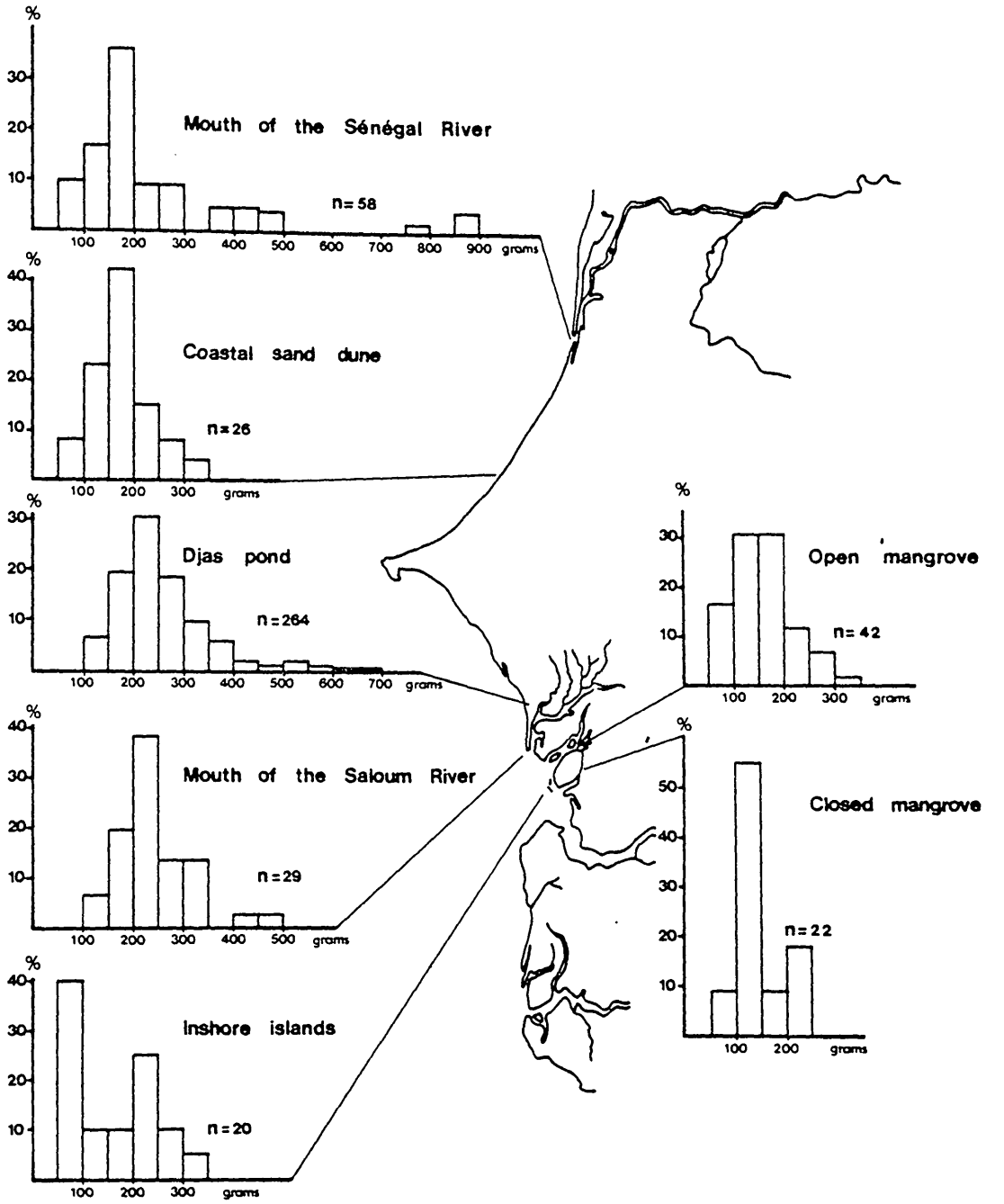

Figure 3.3C Weight distribution of fish caught by Ospreys in Senegambia in April-August.

month	modal length of seine netted fish	average length of fish caught by Ospreys	modal length of fish caught by Ospreys	number of opercula
January-May	200-230	232+-22	240	150
March-May	200	260+-22	260	33
August	200-210	229+-23	240	12
September-October	190-210	264+-28	260	31
November-December	200-230	239+-26	250	15

Table 3.8. Modal and average lengths (mm) of Fimbriated Herring, Ethmalosa dorsalis, caught by Ospreys at the mouth of the Saloum River, and modal length of Fimbriated Herring seine netted at the mouth of the Gambia River (Scheffer and Conand, 1976). The sizes of fish caught by Ospreys were estimated from opercula.

close to the open sea (Figure 3.3A, 3.3B, 3.3C). The highest average weight was along coastal sand dunes during winter, It was lower at sites sheltered from the open sea by offshore sand banks such as at the islands at the mouth of the Saloum River; the lowest was in closed mangrove.

For one fish species, it was possible to examine whether Ospreys caught individuals of different sizes in relation to their abundance in the environment. Scheffer and Conand (1976) studied Fimbriated Herring caught in seine nets at the mouth of the Gambia River, 30 km away from the mouth of the Saloum River, where it was the main prey, and 50 km away from the Djas pond, where it was a major prey. Physical characteristics of these sites were similar. The monthly modal sizes for seine-netted Fimbriated Herring varied between 190 and 230 mm whereas the modal and average sizes of fish caught by Ospreys throughout the year were consistently higher (Table 3.8). The same was true at the Djas pond. These results suggested that Ospreys did not take Fimbriated Herring in proportion to the availability of different size classes, but preferred larger fish.

3.4.4 PREY SIZE AND BIRD SIZE

Size data were obtained for 78 fish caught by marked Ospreys; the weight of each of these birds was determined when they were trapped. The relationship between prey weight and bird weight was examined separately for sites with a high or a low estimated average fish weight. Fish weight and bird weight were significantly correlated

only where fish weight was high ($r=.429$, $p<.01$, $df=62$ for sites with an average prey weight over 240 g; $r=-0.242$, $p>.05$, $df=14$ for sites with an average weight under 240 g).

3.4.5 FORAGING BEHAVIOUR

Ospreys were only observed to catch live fish, and all fish were caught by plunging into water. The height at which they hunted, the angle of penetration, the amount of movement while hunting and the use of hovering, all varied with fish species (Table 3.9). Almost horizontal, shallow dives with considerable manoeuvering and little hovering were used for fast moving fish near the surface such as small mullet and garfish; steep dives (also usually deep), little manoeuvering and frequent hovering were used for slower moving fish not as near the water surface, such as sea bass, Dicentrarchus punctatus, grunts and jackfish. When foraging 1 to 5 km out at sea, for sardines or flying fish, Ospreys often rose up to an estimated height of 300 m, apparently to locate fish, then came down slowly before diving from up to 100 m. In dense mangrove, foraging flights were altogether abandoned, as Ospreys hunted from perches along the edges of the channels.

Two methods were used for Fimbriated Herring. When they were caught out at sea, hunting consisted of a wide ranging search to locate a fish school, punctuated by short hovers; dives were fairly steep and deep. However, herring were also caught in shallow waters at river mouths as they travelled over sand bars between the sea and

fish species	height (meters)	dive angle	speed	range	manoeu-vers	hovering
small mullet	5-15	0-60	fast	small	many	very little
large mullet	5-15	45-75	slow	small	few	little
F. Herring a)	10-20	45-75	slow	wide	few	many
b)	5-15	0-75	slow	small	few	many
garfish	5-40	0-60	fast	wide	many	none
sea bass	5-15	60-90	slow	small	few	many
flying fish	10-40	0-75	slow	wide	few	little
sardine	20-40	60-90	slow	wide	few	many
grunt	20-40	60-90	slow	wide	few	many

Table 3.9. Foraging behaviour of Ospreys according to fish species in Senegambia. Range is the area covered while hunting. It was scored as small when less than 1 km square, as large when more than 1 km square.

the river proper. In these cases, dives were shallow, as the Osprey fluttered down and picked up the fish, barely getting itself wet in the process.

At each study site, foraging behaviour depended on available prey. Since hunts were a series of short visits to different microhabitats within a site, each with its own prey species, foraging behaviour varied accordingly. For example, at the mouth of the Saloum River, mullet were caught close to shore, within the line of breakers, while Fimbriated Herring, in addition to being caught close to shore, were also caught further out at sea. As a consequence, hunts close to shore were lower, involved less hovering, and dives were not as steep or deep as further out at sea.

3.4.6 DAILY FORAGING RHYTHM

Enough data were available to study the daily foraging rhythm at the mouths of the Senegal and Saloum Rivers in January-March.

I could not always monitor the total number of birds foraging at a site, but I could calculate for each hour of the day the average number of minutes when at least one Osprey was observed foraging. Hourly differences in the number of Ospreys foraging were actually more pronounced than in Figure 3.4, since whenever Ospreys were seen foraging for only a small portion of an hour, only one Osprey hunted at any one time, but whenever they were found foraging over most of an hour of observation, then more than one bird usually hunted at any one time.

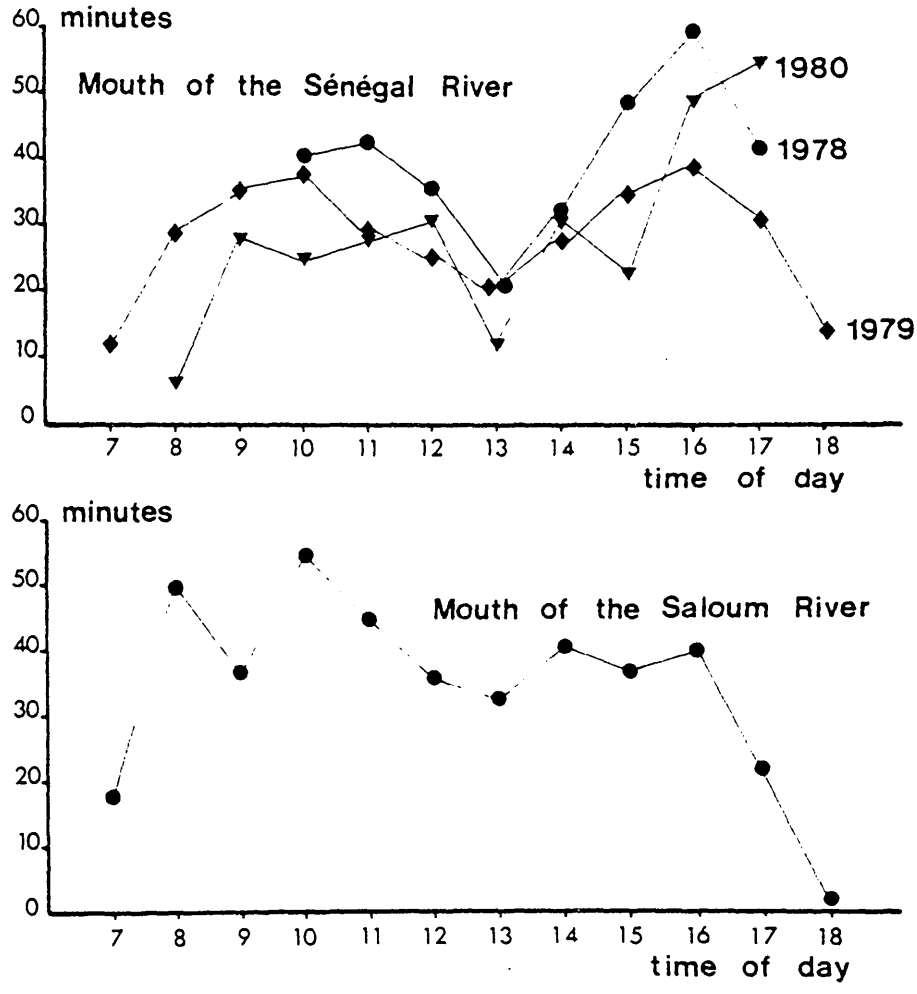

Figure 3.4 Daily foraging rhythm of Ospreys at the mouths of the Senegal and Saloum Rivers.

At the mouth of the Senegal River, there were two peaks, one at mid-morning and a slightly more pronounced one in late afternoon, separated by a period of lower activity from 12:00 to 14:00. At the mouth of the Saloum River, the morning peak was more pronounced and the afternoon peak was almost non existent. Foraging started a little after sunrise, at 7:00, at the mouth of the Saloum River, but was often delayed by thick fogs at the mouth of the Senegal River. Very little foraging was observed in the hour prior to sunset at 19:00. The morning peak could best be explained by hunger after a night without food and the late afternoon peak as food intake before the night or hunger as the first fish was digested. However, I cannot explain the absence of a significant afternoon peak at the mouth of the Saloum River. I will discuss later whether peaks in foraging activity were related to fish availability.

3.4.7 SOCIAL BEHAVIOUR WHILE FORAGING

Wintering Ospreys were very tolerant of each other at foraging sites. At the mouth of the Saloum River, up to 22 Ospreys were observed perched within a 100 meter circle, some only 1 or 2 meters apart, and up to 16 were observed foraging over an area of about four hectares. There was occasionally a clear social component to foraging behaviour: Ospreys that started foraging usually did so near Ospreys already foraging, and after a lull in foraging, one Osprey often stimulated others to hunt. For example, on 25 March 1979, 12 Ospreys were perched at the mouth of the Saloum River.

Another Osprey foraged and caught a Fimbriated Herring from a school passing in shallow waters. Three Ospreys immediately flew off, two of which caught a fish in the following minute. Two more Ospreys then flew off, one of which caught a fish in 4 minutes. Another then flew off and two Ospreys caught a fish in the following 2 minutes. Another then flew off and one Osprey caught a fish in the following minute. Two minutes later another flew off to join the last Osprey hunting and these two, probably too late, did not catch any fish. There was thus a clear advantage in going immediately to where a bird had been successful. All the hunting took place over the spot where the first Osprey had caught a fish. Behaviour like this was frequent at the mouth of the Saloum River where birds hunted in a well defined and restricted area, less so at the mouth of the Senegal River, where birds hunted over a wider area and birds were more dispersed.

No attempts by an Osprey to rob another Osprey of its fish were observed at the mouth of the Saloum River, the site with the highest Osprey densities, but seven attempts were observed at the mouth of the Senegal River. These consisted of a close pursuit lasting up to 1 minute, but in only one case did the victim let go of its fish which was not then recovered by the aggressor. On another occasion in the mangrove of the Saloum River delta, an Osprey joined a Palm Nut Vulture, Gypohierax angolensis, in pursuit of an Osprey, forced the victim to drop the fish but did not recover it. Still another unsuccessful attempt was observed along the coastal sand dunes

between the mouth of the Senegal River and the Cap-Vert peninsula. These attempts were relatively few when compared with the over 800 successful captures observed. To conclude, Ospreys were generally indifferent to each other, but occasionally took advantage of one another to find food.

3.4.8 FORAGING SUCCESS

3.4.8.1 Winter

Results are available throughout the winter for three sites, the mouths of the Senegal and Saloum Rivers and inshore islands (Table 3.10). Dive success was on average lower in October-December than in January-March, (mouth of the Senegal River, chi-square=35.3, df=1, $p<<0.05$; mouth of the Saloum River, chi-square=22.8, df=1, $p<<0.05$; shallow coastal tidewaters, chi-square=4.19, df=1, $p>.05$; inshore islands, chi-square=1.9, df=1, $p>0.05$; mangrove, chi-square=1.8, df=1, $p>0.05$) while time per capture showed no consistent pattern.

The three groups of observations at the mouth of the Senegal River in October-December were in three different microhabitats: (1) a pocket of clear freshwater in a cul-de-sac south of the river mouth, (2) fresh floodwater laden with silt, and (3) clear seawater to the north of the floodwater plume. Most of the Ospreys foraged at the pocket of clear freshwater, where time per capture was lowest.

There was no consistent pattern in January-March at the mouth of the Senegal River: in 1979, dive success increased from 34% to 42%

site		average time per capture in minutes	% dives successful (number of dives)
OCTOBER-DECEMBER			
Coastal sand dunes		20.1	34 (41)
Mouth of the Senegal River			
clear freshwater		12.9	20 (114)
floodwaters		20.5	17 (121)
clear sea water		23.8	29 (48)
Mouth of the Saloum River		30.0	18 (146)
Inshore islands		38.5	12 (26)
Shallow coastal tidewaters		14.1	28 (50)
Mangrove		17.8	18 (17)
JANUARY-MARCH			
Coastal sand dunes		63.1	39 (18)
Mouth of the Senegal River	1978	23.6	44 (150)
	1979	33.3	34 (323)
	1980	25.0	39 (315)
Mouth of the Saloum River	1978	20.9	34 (150)
	1979	20.3	36 (341)
Inshore islands	1978	30.2	22 (241)
	1979	16.7	25 (298)
Shallow coastal tidewaters		19.7	52 (21)
Mangrove		15.6	41 (17)

Table 3.10. Foraging parameters of Ospreys in Senegambia in winter.

from February to March (chi-square=0.33, df=1, $p>0.05$), but in 1980 it decreased from 50% to 33% in the same period (chi-square=9.44, df=1, $p<0.05$). In 1978, it was 44% in March. These changes were difficult to interpret. The instability of the habitat might have affected fish accessibility: in 1978, there was a single narrow outlet to the sea, in 1979 another outlet was formed with an island between the two outlets and in 1980 the island between the two outlets was washed away, leaving a 2 km wide outlet.

At the mouth of the Saloum River, dive success increased during the season and time per capture decreased: from January to March 1978 dive success went from 30% to 38% (not significant, $p>0.05$), time per capture from 26,1 minutes to 17,3 minutes; from February to March 1979 dive success went from 34% to 38% (not significant, $p>0.05$) time per capture from 26,8 to 17,1 minutes. Around inshore islands, dive success was similar in both years, but time per capture was almost twice as long in 1978 as in 1979.

Observations from three other sites are also reported in Table 3.10, though sample sizes were much smaller. Note the high time per capture along coastal sand dunes in January-March.

3.4.8.2 Summer

Only a few observations were available for nonbreeding (mainly immature) Ospreys in April-August when breeding birds were in Europe (Table 3.11). In general, foraging parameters were slightly improved over those observed in winter.

site	average time per capture in minutes	% dives successful (number of dives)
Mouth of the Senegal River	17.5	40 (15)
Mouth of the Saloum River	16.1	36 (28)
Shallow coastal tidewaters	20.5	25 (8)
Inshore islands	11.1	29 (7)
Mangrove	27.6	29 (14)
TOTAL	18.3	33 (72)

Table 3.11. Foraging parameters of Ospreys in Senegambia in April-August.

3.4.8.3 Variation with prey characteristics

Dive success might be expected to vary with fish weight. A large target is easier to catch than a small one of similar shape, the only constraints being that very small fish might be missed altogether and fish over 400 grams cannot always be lifted out of the water. In the latter cases, the Osprey will lie on the water, wings opened, for up to two minutes, in the end releasing the fish or the fish wriggling itself free.

The relation between dive success and fish size was tested by regressing dive success on average estimated weight of fish actually caught (Figure 3.5). The data used came from different sites during winter; summer data were excluded because only immatures were involved and sample sizes were too small. Dive success was significantly correlated with fish size ($r=0.56$, $p<0.05$, $df=14$).

The average time per capture at a site might be expected to be correlated with average fish weight because small fish were more abundant than large fish so that quick capture of large fish was unlikely, even when large fish were preferred. In addition, Ospreys might abandon sites where they could only capture small fish slowly. As predicted, average time per capture was significantly correlated with average fish weight (Figure 3.6) ($r=0.56$, $p<0.05$, $df=14$). However, there was no significant correlation ($p>>0.05$) when I removed the data point for the coastal sand dunes between the mouth of the Senegal River and the Cap-Vert peninsula (time per capture 63.1 minutes, average weight 414 g).

Although dive success and average time per capture were both significantly correlated to fish weight, they were not significantly correlated with each other ($r=-0.01$, $p>>0.05$, $df=14$).

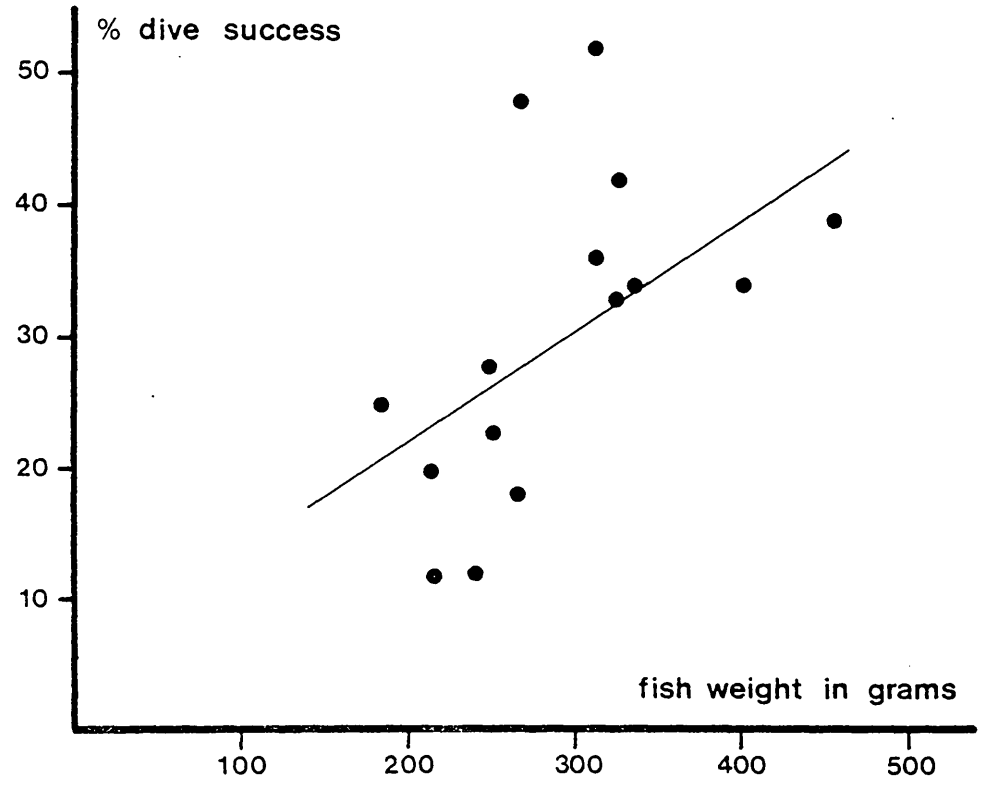

Figure 3.5 Dive success vs average weight of fish for Ospreys in Senegambia.

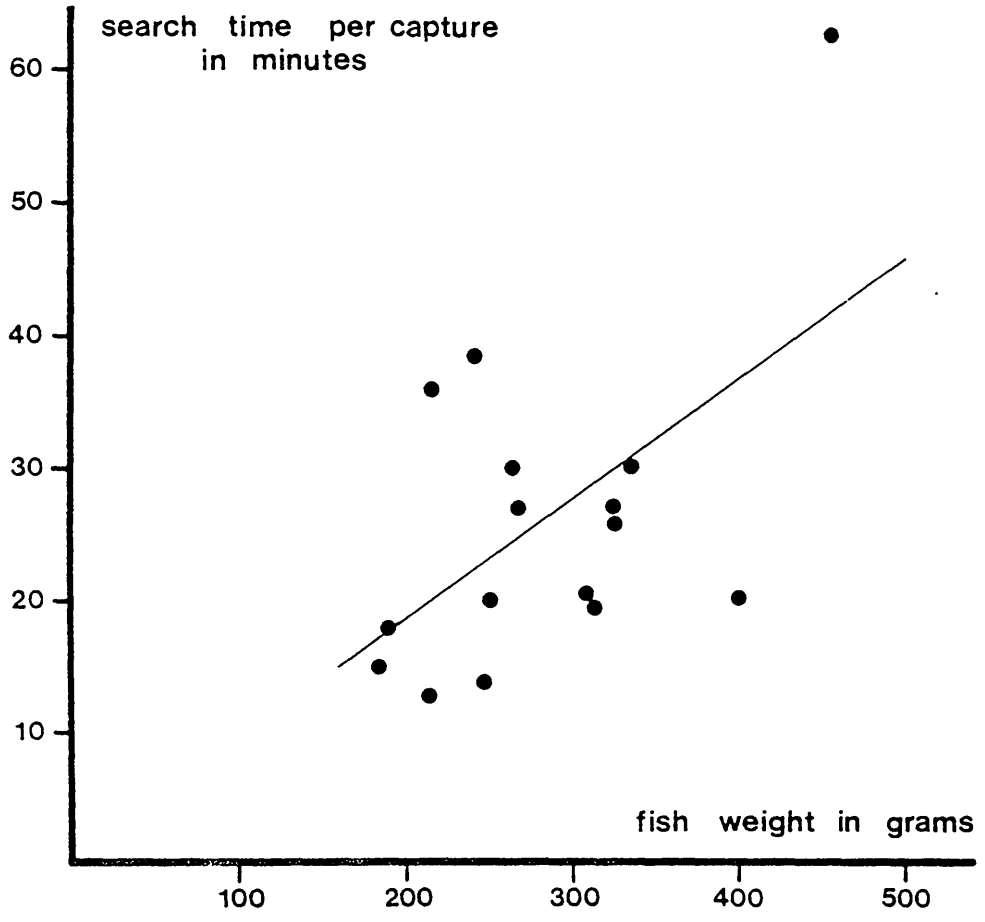

Figure 3.6 Average time per capture vs average weight of fish for Ospreys in Senegambia.

	average time per capture in minutes	% dives successful (number of dives)
OCTOBER		
Immatures 2 months	34.5	7 (16)
Others	9.1	27 (30)
FEBRUARY-MARCH		
Immatures 6 months	33.9	19 (42)
Others	22.9	40 (67)

Table 3.12. Foraging parameters for different age classes of Ospreys at the mouth of the Senegal River. Age is given from a fledging date of 1 August.

3.4.8.4 Variation with age classes

Foraging parameters also varied between age classes. Sufficient observations were made on marked individuals at the mouth of the Senegal River to compare immatures and older birds (Table 3.12). Data for October are few and must be interpreted with caution. Data for February-March show that immatures 6 months old had a significantly lower dive success than older birds (chi-square=4.61, $p<.05$, df=1), although time per capture was not correspondingly higher: this is because the time per dive was lower for immatures 6 months old than for older birds (6.5 minutes versus 9.2 minutes), implying that older birds were better at judging when success was possible.

3.4.8.5 Variation with time of day

Foraging parameters apparently did not vary with time of day (Table 3.13). There was no significant variation in dive success at different times of the day at the mouth of the Senegal River in February-March 1980 (chi-square=10.218, df=9, $p>.3$) and, although time per capture could not be tested statistically, it followed no clear trend. In particular, dive success was not lower and time per dive was not higher during the period of lowest activity from 12:00 to 14:00 (Figure 3.4). If Ospreys had foraged when fish were most available, I would have expected a negative correlation between the extent of Osprey foraging (as in Figure 3.4) and the time per capture. This was not the case ($r=.21$, df=9, $p>>.05$), and there is

	time of day									
	8	9	10	11	12	13	14	15	16	17
Dive success (%)	25	43	47	18	43	33	30	29	46	27
Number of captures	1	16	15	4	10	3	8	11	23	6
Time per capture	18.7	21.5	26.0	72.1	20.4	29.0	30.1	23.6	23.4	41.0
	\ /		\ /		\ /		\ /		\ /	
	21.3		35.7		22.4		26.3		27.1	
Activity index	6	23	25	28	31	12	32	23	48	55

Table 3.13. Dive success and time per capture at different times of the day at the mouth of the Senegal River in February and March 1980. The activity indices taken from Figure 3.4 for the mouth of the Senegal River in 1980.

no reason to assume that foraging success had any systematic relationship to time of day.

3.4.9 ENERGETICS

In this section, I shall discuss Osprey energetics in Senegambia and estimate the foraging time required to meet daily energy requirements.

Fish flesh is made up mostly of water (65-85%), proteins (15-20%) and lipids (0-15%); the carbohydrate content is usually around 1%, a negligible fraction (Sidwell *et al.*, 1974). Proteins provide metabolizable energy at 4.2 kcal per g and lipids at 9.5 kcal per g (King and Farner, 1961), where metabolizable energy comprises the net energy available to the animal for locomotion, maintenance, moult, and storage of fat or protein reserves, together with the energy transformed into heat following the assimilation of food (specific dynamic action, SDA). The SDA varies with the type of food consumed and the use made of it. For maintenance and locomotion, 28% of metabolizable energy from proteins and 5% from lipids is lost as SDA; for putting on fat, such as before migration, 35% of metabolizable energy from proteins and 10% from lipids is lost as SDA (De Groote, 1974).

The net energy available from fish varied mainly according to lipid content (Table 3.14). Species such as mullet and Fimbriated Herring which had high lipid contents, had the highest calorific values. The proportion of the fish that was edible also varied with

species	% protein	% lipid	net energy kcal per 100 g	% edible portion
Sardinella aurita	20.5	3.8	102	65
Sardinella maderensis	19.0	3.7	96	65
Ethmalosa dorsalis	20.0	2.0	84	65
Exocoetidae	20.1	1.1	76	
Belonidae	23.2	1.1	86	60
Mugil cephalus	19.4	5.5	113	52
Mugilidae	19.2	3.3	93	
Cichlidae	14.2	6.7	107	38
Ariidae	18.3	1.2	71	
Serranidae	18.6	1.6	75	50
Pomadasydae	19.2	0.9	71	50
Caranx spp.	19.9	1.2	76	

Table 3.14. Net energy available for maintenance and locomotion per 100 g fresh flesh of fish taken by Ospreys in Senegambia.
Values for metabolizable energy are 4.2 kcal per g of protein and 9.5 per g of lipid (King and Farner, 1961). Conversion factors from metabolizable energy to net energy available for maintenance and locomotion are 0.78 for proteins and 0.95 for lipids (de Groote, 1974). Values for % protein and % lipid from Sidwell et al. (1974) except for Cichlidae which is adapted from Tan (1971). Edible portion from Edwardson (1976) for Cichlida e and fro m Bell and Canterbury(1976) for Mugilidae.

species (Table 3.14): the unedible fraction included the head, guts, skeleton, skin and fins.

Although fish size ranged up to one kilogram, fish over 400 g were not fully eaten, and occasionally only 100-200 g were eaten from fish over 500 g before they were discarded. Because of this, the weight of fish over 400 g was set at 400 g in the following calculations.

In a number of instances, observations of foraging and diet were both available, permitting me to calculate Osprey foraging efficiency as the rate of capture of net energy in kcal per minute of foraging (Table 3.15). Foraging efficiency ranged from 2.9 to 10 kcal per minute of foraging but there was no clear seasonal trend. It was lowest in mangrove during the summer when only immatures where present and along coastal sand dunes in February-March. It was highest for Ospreys feeding on flying fish along coastal sand dunes in December.

The basal metabolic rate (BMR) is the rate of consumption of net energy. It is measured with the animal at rest, in thermoneutral conditions, and in a post-absorptive state (Gessaman, 1973; Kendeigh et al., 1977). The BMR of the Osprey is 3.2 kcal per hour per kg (Wasser, 1979). According to Mosher and Matray (1974), sexual dimorphism in birds of prey does not lead to differences in metabolic rate per gram of body weight. Since the weight of Ospreys in this study varied from 1.3 to 2kg, their BMR was assumed to vary from 4.1 to 7.3 kcal per hour.

The lower limit of thermoneutrality of Ospreys, at 22.6 degrees C, is high compared to other raptors (Wasser, 1979). However, this does not imply that a free-living Osprey must spend energy to maintain body temperature whenever the ambient temperature falls below 22.6 degrees C. Fish are high in protein and the assimilation of protein releases considerable heat which can be used for thermoregulation (Kendeigh et al., 1977). In view of this, and since the average daily temperature in Senegambia does not fall below 20 degrees C, I shall assume that no energy was spent in thermoregulation, even at night.

Wintering Ospreys divided their day into roosting at night (12 hours), flying between the roost and the foraging site and flying at the foraging site while not hunting (I estimated one half hour of such flying), hunting (y minutes), and resting at the foraging site (11.5-y/60 hours).

The energy expended while roosting was assumed to be equal to BMR. The energy expended for resting in various birds studied ranged between 1.2 and 1.8 BMR (King, 1974). I used the average value of 1.5 BMR to estimate the energy expended by an alert Osprey resting at a foraging site during the day. Values for the energy expended in flight have been found to range between 4X and 17X BMR, averaging about 10-12X BMR (King, 1974). Energy expenditure in directed flight was assumed to be 10 BMR, while expenditure during hunting was assumed to be 15 BMR, because of the manoeuvering, hovering and diving involved. Since the daily expenditure of energy consisted of

site	average time per capture in minutes	average net energy content of fish in kcal	foraging efficiency in kcal per minute	time to meet daily requirements in minutes
Coastal sand dunes				
February-March	63.1	<200	<3.2	63-165
November	20.1	200	10.0	16-30
Mouth of the Senegal River				
February 1979	30.2	162	5.4	32-67
March 1979	27.1	143	5.3	32-69
February 1980	24.0	153	6.4	26-53
March 1980	25.8	139	5.4	32-67
April-August	17.5	121	6.9	24-48
October a)	12.9	116	8.4	19-37
October b)	20.5	119	5.4	32-67
October c)	23.8	123	5.2	33-71
Mouth of the Saloum River				
March	16.5	160	9.7	16-31
October	30.0	154	5.1	34-72
Inshore islands				
February	17.0	97	5.7	30-61
March	16.4	103	6.3	26-54
November	38.5	130	3.4	57-145
Shallow coastal tidewaters				
October	18.0	130	7.2	22-45
December	16.4	127	7.7	21-41
January	19.7	155	7.9	20-40
Mangrove				
April-August	27.6	77	2.8	75-220
November	17.8	95	5.3	32-68

Table 3.15. Foraging efficiency of Ospreys at various sites in Senegambia.
The lower value for the time needed to meet daily requirements value is for Ospreys weighing 1.3 kg, the upper value for Ospreys weighing 2.0 kg. The average calorific content of fish is the average of calorific contents for each fish species. This in turn is the product of the average weight, fish over 400 g are corrected to 400 g, by the calorific value and the edible portion as in Table 3.14.

1) Energy + Energy + Energy + Energy
roosting flying hunting resting

then if we substitute the assumed values

2) 12*BMR + .5*10*BMR + y/60*15*BMR + (11.5-y/60)*1.5*BMR =
daily energy expenditure

Given a foraging efficiency (FE) in energy per minute, as in Table 3.15, then the daily energy requirements will be met if the daily energy expenditure equals the daily energy capture (y*FE). The equation can be solved for y.

3) $$y = 60 * \frac{34.25*BMR}{60*FE - 13.5*BMR}$$

Equation 3) was solved for the foraging efficiency values in Table 3.15, providing us with estimates of the foraging time needed to meet daily energy requirements for maintenance and locomotion.

Given the various assumptions mentioned above, the hunting time needed to meet daily requirements varied from 16 to 70 minutes (mostly under 30 minutes) for Ospreys weighing 1.3 kilograms and from 30 to 195 minutes (mostly under 60 minutes) for Ospreys

weighing 2.0 kilograms. This corresponded to a daily energy expenditure of 155-205 kcal per day for an Osprey of 1.3 kilos (the size of a male) and of 299-570 kcal per day for an Osprey of 2.0 kilos (the size of a female).

3.5 DISCUSSION

3.5.1 PREY SELECTION

Ospreys were not seen to go further than 8 km out to sea to hunt; therefore pelagic species, found further away from shore, were excluded from their diet. Such species included the tuna like fish such as the Scombridae, the Thunnidae, and the Cymbiidae, and the Carangidae, such as Trachurus spp..

There was also a limit to how deep Ospreys could dive. Thus few demersal fish, accessible to Ospreys only if they came to shallow waters or near the surface, appeared in the diet. Such species included: croakers, Pseudotolithus spp., catfish, plexiglas nosed fish, Galeoides decadactylus, barracuda, Sphryaena spp., and groupers, Epinephelus spp..

Compilations of commercial catches gave some idea of what other species were abundant in the zone visited by Ospreys. The Centre de Recherche Oceanographique de Dakar Thiaroye (CRODT, 1979) gave the following species as the most important commercial fish in coastal waters: sardines, Fimbriated Herring, various Carangidae, grunts,

especially Pomadasys jubelini, and mullet of the genera Mugil and Liza.

Although Carangidae, such as Chloroscombrus chryusurus and Caranx rhonchus, inhabited coastal waters, they were of little importance to Ospreys, because they did not normally live in shallow waters or come near the surface. The other species in the CRODT list formed the bulk of the diet. Four less important species or species-groups were also taken by Ospreys: (1) flying fish which were not important commercially because they could fly over most fishing nets; (2) sea bass, although not very abundant in absolute terms, were caught by Ospreys because young fish live in breakers along the coast; (3) garfish, a predator of small fish, abundant in shallow waters where small mullet and Fimbriated Herring were found; (4) tilapia, found in ponds and estuaries, occasionally in the open sea. Although these species were not as abundant in coastal waters as the commercially important species listed above, they behaved in ways that made them vulnerable to Ospreys. Thus the diet of Ospreys consisted partly of the most abundant fish species in coastal waters and partly of less abundant species whose behaviour made them particularly available.

As a group, mullet were the main prey. These fish lived in waters as shallow as 50 cm and travelled in schools near the surface. In estuaries they were the fish most often caught by fishermen; they were the most numerous fish in seine nets pulled in shallow waters and the most common fish, often the only fish, caught in throw nets

from the shore.

Mullet species varied in their distribution and abundance (Cadenat, 1954): each species had a particular tolerance to water salinity (Payne, 1976) and temperature which limited its distribution; each species also had microhabitat preferences for the particle size of the substrate (Blaber, 1977), which were related to the mode of feeding (Payne, 1978).

The available information on the distribution and behaviour of the mullet in Senegambia was insufficient to explain in detail the diet of Ospreys. However, as no discrepancy was noted between the diet of Ospreys and catches by local fishermen, or the knowledge of fish biology shown by these fishermen, it was likely that the diet reflected accessible fish, within certain size limits, in the habitats where Ospreys hunted. Any assumption of prey species preference by Ospreys on other criteria would seem unjustified.

There were sudden changes in prey species composition with time, the best examples of which were the frequent daily shifts between a diet of Fimbriated Herring and mullet and a diet of flying fish at the mouth of the Senegal River and at shallow coastal tidewaters near the Djas pond. Whereas Fimbriated Herring and mullet were caught in shallow waters, flying fish were caught out at sea where they became more available whenever they drifted closer to shore. Therefore, the shifts in prey species were not prey switching as understood by Murdoch (1969), where a predator attacks disproportionately the most abundant prey of a habitat, but instead

resulted from habitat changes, the most profitable habitat at any one time apparently being preferred. Other less sudden shifts in prey species were related to absolute changes in abundance of the species concerned because of their migrations.

Since Africa and Europe have different fish faunas, the species taken by Ospreys in the two regions were consequently different. However, in both areas the main prey were the most common primary consumer, mullet in Senegambia, Cyprinidae in Europe (Hakkinen, 1978). Elsewhere along the coast of West Africa, from Mauritania to Gabon, mullet are also likely to be the main prey species, while in fresh water habitats, such as the inner delta of the Niger River, tilapia are probably the main prey.

3.5.2 PREY SIZE SELECTION

Although there was no sign of a preference for a particular prey species, there did appear to be a preference for prey size. In theory, small individuals were more abundant than large ones in the fish populations, but this was not the case with the fish caught by Ospreys. Most fish taken were between 200 and 300 grams, very small fish were not represented, and large fish were over-represented. This is well illustrated by the data from the Langue de Barbarie (Table 3.3), and by data for Fimbriated Herring caught by Ospreys at the mouth of the Saloum River and at the Djas pond. That birds selected fish size was also suggested by the significant correlation between fish weight and bird weight at sites where fish size was

large enough for a size preference to be shown. Presumably, at sites where average fish weight was under 250 grams, such as in mangrove, Ospreys would have taken larger fish if these had been available.

The range of fish weights was similar in Senegambia to that found on the breeding grounds of Europe and North America, (Schnurre, 1961; Nordbakke, 1974; Prevost, 1977; Hakkinen, 1978; Swenson, 1978), but average fish weight was higher in winter than on the breeding grounds.

3.5.3 FORAGING SUCCESS

The Osprey foraging parameters observed in this study fell within the range observed on the breeding grounds of Europe and North America (Table 3.16), but on average dive success was lower and search time per capture was higher. Foraging parameters have been shown to vary with weather (Grubb, 1977; Prevost, 1977; Ueoka and Koplin, 1973) but they vary much more between sites than expected from weather alone. Swenson (1978) showed that dive success correlated well with prey type; it was lowest for fast moving, somewhat slim fish, such as Northern Pike, Esox lucius, and highest for stationary, wide bodied fish such as flounders, Pleuronectidae. Dive success at each site in this study was presumably the average of different rates of success for each fish species and fish size at that site. Dive success was significantly lower when fast moving small mullet were caught (10-25 %), than the slower larger mullet

site (reference)	fish species	dive success (no of dives)	average time per capture in minutes
Florida (Nesbitt, 1974)	sunfish	28 (50)	-
Norway (Nordbakke, 1974)	orfe, pike, perch	34 (116)	-
Finland (Prevost, unpub.)	rainbow trout	44 (677)	17.4
Florida (Grubb, 1977)	mulet, crappie	44 (283)	10.5
Yellowstone Lake) (Swenson, 1978)	trout	47 (153)	12.4
Yellowstone River (Swenson, 1978)	trout	48 (33)	-
North California (Garber, 1972)	chub, trout	56 (36)	-
Idaho (Schroeder, 1972)	---	57 (21)	-
North California (Ueoka, 1973)	surfperch	58 (1974)	-
Montana (MacCarter, 1972)	sucker, whitefish	65 (132)	-
Scotland (Prevost, unpub.)	flounder	65 (44)	19.2
Upstate New York (Singer, 1974)	---	65 (23)	-
Oregon (Lind, 1976)	trout, chub	68 (60)	-
Nova Scotia (Prevost, 1977)	winter flounder	69 (2268)	9.5
North California (French, 1972)	smelt	69 (144)	8.2
Nova Scotia (Lambert, 1943)	---	90 (469)	-
Florida (Nesbitt, 1974)	shad	91 (29)	-

Table 3.16. Foraging success of Ospreys in Europe and North America. The average time per capture includes time spent foraging by Ospreys that afterwards quit without catching a fish.

and Fimbriated Herring (30-50 %).

The foraging success of immatures and adults has been compared in the Royal Tern, Sterna maxima, (Buckley and Buckley, 1974) and the Sandwich Tern, Sterna sandvicensis, (Dunn, 1972). In both birds, foraging success was lower in immatures than in adults (Table 3.17). In Royal Terns, adults foraged over a given stretch of beach at about twice the speed of juveniles and hovered precisely over the intended dive spot before plunging neatly into the water, while immatures repeatedly circled back and forth over an area, making many intention movements to plunge, finally flopping obliquely into the water. In Sandwich Terns, juveniles dived from a lower height than adults, with less speed and penetration into the water. However, the manner in which foraging parameters improved with age differed between these species. In Royal Terns, dive success was identical between age groups, while average time per dive was higher in immatures; in Sandwich Terns, the average time per dive was identical, but dive success was lower in immatures. The ability to capture fish was more quickly learnt than the ability to locate prey in the Royal Tern, while the opposite was true in the Sandwich Tern.

According to Table 3.12, the foraging success of Ospreys 6 months old was still significantly lower than that of adults at the mouth of the Senegal River, although the difference was slightly less than that observed between fledglings and adults by Szaro (1978)(Table 3.17). Immatures 6 months old dived more frequently than adults, but with only half the dive success, a pattern also apparent in

species (reference)	age class	average time per capture in minutes	average time per dive in minutes	proportion of dives successful
Sterna maxima				
(Buckley and	adults	5.3	1.7	37.6
Buckley, 1974)	<12 months	13.7	2.7	37.7
Sterna sandvicensis				
(Dunn, 1972)	adults	3.6	0.6	13.5
	<12 months	6.1	0.6	9.7
Pandion haliaetus				
(Szaro, 1978)	adults	38.3	7.1	18.6
	fledgings	77.3	6.1	7.9

Table 3.17. Foraging success of adult and immature fish-eating, diving birds previously reported in the literature.

Szaro's data for fledglings. There were no apparent differences between age classes in diving technique or foraging height, such as those reported by Dunn (1972) and Buckley and Buckley (1974) for terns. Part of the improvement in foraging success probably came from improved ability to capture. However, the less frequent dives of adults show that learning when not to bother to dive was important, and this factor can also explain the improvement in dive success.

Since dive success and time per capture were not related to time of day, the hunting schedule of Ospreys in Senegambia seemed mostly determined by hunger. This schedule was not limited by the amount Ospreys could eat in a meal: they can eat more than 300 g of fish flesh within a few minutes (Prevost, unpub.). Therefore there was no bottleneck that forced them to spread meals over a day.

3.5.4 FORAGING EFFICIENCY

Ospreys in Senegambia needed only 20 to 60 minutes of foraging to meet their daily requirements. The rest of the day was spent eating, digesting, preening and resting at the foraging site. Meeting the requirements meant eating 1-3 fish per day, depending on fish size. However, foraging efficiency was not inversely correlated with fish size because, whenever fish were small, less time was required to catch them.

It was surprising that most Ospreys were found in mangrove where foraging efficiency was lower than along the coast. However, most

Ospreys in closed mangrove hunted from perches in which case the measure of foraging efficiency that I used was not valid. The energy expended hunting from a perch would have been little above that while resting and, by avoiding active hunting, a bird greatly reduced its daily energy requirements relative to the requirements of birds on the coast, even if fish were less abundant in closed mangrove. However, when mud flats in closed mangrove were exposed at low tide, Ospreys could no longer forage from channelside perches. Presumably birds that had not caught a fish left for more open mangrove, while birds that had eaten earlier that day stayed in the closed mangrove.

Wakeley (1978) observed that Ferruginous Hawks, Buteo regalis, preferred hunting from a perch to hunting from flight, even though the ratio of captures to capture attempts and the capture rate were higher when hunting from flight. Similar observations were reported by Tarboton (1978) for Black Shouldered Kites, Elanus caeruleus. Wakeley speculated that (a) there was no pressure to increase the capture rate because daily food requirements were easily met even when hunting only from a perch, and (b) hunting from a perch resulted in a greater number of captures per unit of energy expended because of the low metabolic cost of this method relative to that of hunting from flight. Wakeley's assumptions are equivalent to saying that daily energy requirements are minimized relative to foraging method as long as enough food is obtained to meet requirements.

However, Wakeley (1978) and Tarboton (1978) had to assume that

hunting method was not selective for prey size; for example, hunting from flight might have yielded larger prey. In Senegambia, fish were definitely smaller in closed mangrove than elsewhere. Nevertheless, Ospreys seemed to prefer hunting from perches in closed mangrove to active foraging elsewhere, in accordance to Wakeley's and Tarboton's observations.

The highest value for foraging efficiency was observed in December along coastal sand dunes between the mouth of the Senegal River and the Cap-Vert peninsula when flying fish were the main prey, but this was temporary: foraging efficiency was much lower in late winter after the flying fish had departed and probably also before they arrived in December. However, foraging efficiency was more stable at the mouths of the Senegal and Saloum Rivers and at shallow coastal tidewaters near the Djas pond. Accordingly, more Ospreys were found at these three sites than elsewhere along the coast even though they comprised less than one quarter of the coastline.

CHAPTER 4

THE MOULT OF THE OSPREY

4.1 INTRODUCTION

Few detailed studies of moult have been made on large birds. The Stresemanns (1966), reviewing the moult of primaries in a large number of species, found that large birds have moult patterns different from those of smaller species, in that two or more primaries moult at the same time at different positions along the wing. This they termed the serial moult or Staffelmauser. Dorward (1962), working with marked Blue-faced Boobies Sula dactylatra, was the first to show how such a pattern develops. The pattern has also been described in detail for the Fairy Tern, Gygis alba (Ashmole, 1968), the shag, Phalacrocorax aristotelis (Potts, 1971), and the White Stork, Ciconia ciconia, (Bloesch et al., 1977).

According to Stresemann (1960), the Osprey has an irregular moult sequence of the primaries, later shown to be a Staffelmauser by Edelstam (1969). Edelstam (in Glutz Von Blotzheim, 1971) also reported on the timing of moult: feather replacement was most active from July to early September and from mid-October to March, stopping during migration to the breeding and wintering grounds. This

chapter describes primary moult in the Osprey, shows how the moult pattern develops, and discusses the factors that have lead to its evolution. It is based on observations of marked Ospreys captured in the field and of museum specimens.

4.2 METHODS

Field work was in 1979-80 along the coast of Senegambia. During the study, 120 Ospreys were caught with snare traps set on feeding perches; 22 of these were captured twice and 5 three times, giving a total of 147 observations. Eleven of the Ospreys had been ringed as nestlings, 5 in Finland, 5 in Sweden, and 1 in Norway. The other Ospreys were marked, when first captured, with rings provided by the Museum d'Histoire Naturelle de Paris.

I preferred to use the term moult wave (Ashmole, 1968) for a single sequence of moult travelling along a feather series rather than moult cycle (Potts, 1971), because of the possible confusion of the latter with the period available for moult within the annual cycle (as in Palmer, 1972). The terminology of Humphrey and Parkes (1959) for plumages is not used as it is not convenient for birds with a Staffelmauser. Moult of the primaries will be described by the number of waves completed and in progress. Moult front designated the leading edge of a moult wave and was said to be active if any feather was missing or growing, dormant if not. A

missing feather was considered to be moulting (Watson, 1963). If the primary preceding another in a series was appreciably older, suggesting that moult had been interrupted, this was called a discontinuity. Moulting period designated the time between interruptions, i.e. contiguous feathers in a wave that showed no discontinuity were ascribed to the same moulting period.

Individual primaries were referred to by using the letters L or R (left or right) and numbered from 1 to 10 from the innermost outward.

For each capture, the growth stage of each of the primaries and rectrices (secondaries in 126 cases) was scored on a scale of 0 to 5 (Ashmole 1962 and others) as follows: 1- missing feather, 2- pin feather or small brush, 3- large brush to half grown, 4- half grown to 3/4 grown, and 5- 3/4 grown to fully grown feathers. Feathers from previous moulting periods were scored as 0, though this was difficult late in the current moulting period, when the first feathers to have moulted were not always separable from feathers replaced late in the previous moulting period. Growing feathers were also measured to the nearest 1 mm with a thin plastic ruler placed against the base of the feather. This permitted me to calculate average daily feather growth on the few Ospreys retrapped within a short time span.

The primary moult score for each wave was computed by scoring five points for each of the primaries replaced by the wave and adding the appropriate moult scores for any growing feather. Both wings were

considered and the completed moult score for a wave was 100 (10 primaries per wing). In certain Ospreys, I could determine the number of moult waves completed since fledging. The history of the primary moult of a bird was then described by listing the scores for all the moult waves completed and in progress. Moult described in this way might have extended over more than one moulting period. As an example consider an Osprey that had completed one moult wave, had its second moult wave at primary 9 (fully grown in both wings) and its third moult wave at primary 3 (fully grown in both wings). This moult would then be noted as (100, 90, 30) and the cumulative moult score in this instance would be 220.

The primary moult score for a moulting period was calculated as in Ashmole (1968): moult scores of feathers moulted in that moulting period were computed for each wave and then summed. Scores within a moulting period (both wings) varied from 0 (no moult) to 100 (all primaries replaced). Secondary and tail moult scores for a moulting period were similarly calculated but on the basis of 18 secondaries for each wing and 12 tail feathers.

In this paper, I follow the recommendation of Ginn (1975) and Pimm (1976) to use date as the dependent variable in linear regressions between moult scores and dates. They found that regressions with date as the independent variable give too long an estimate of moult duration because the slope is affected by the variability of starting dates; however, if date is used as the dependent variable then the regression line correctly estimates the duration of moult,

and variance about this line is a measure of the variability of the starting date.

A second scoring system was used to denote the age of feathers. For each capture, feather wear of the primaries and rectrices (secondaries in 126 cases) was scored on a scale of 0 to 9: 0- missing or growing feather, 1- new feather, 2 to 8- increasingly worn and discoloured feathers, and 9- like 8 but with the rachis broken as well. Patterns of previous moults were visible from these scores.

Age was given in months starting from a fledging date of 1 August. The term immature was used for Ospreys that had not yet made their first spring migration and adult was used for Ospreys that had presumably returned at least once to their breeding grounds.

Osprey skins were examined at the American Museum of Natural History in New York, at the Smithsonian Institution in Washington, at the British Museum (Natural History) in Tring, and at the National Museum of Natural Sciences in Ottawa. Moulting (i.e. growing or missing) primaries were noted for adult Ospreys of known sex collected on the breeding grounds; 55 specimens were available of Pandion haliaetus carolinensis and 21 of Pandion haliaetus haliaetus.

4.3 RESULTS

4.3.1 BIRDS OF KNOWN AGE

Ospreys fledged in the previous summer were recognizable when they first arrived in winter quarters by their speckled plumage, with light tips on the dark feathers of the wings, back and tail, and in the hand by the uniform wear of the flight feathers. The speckled aspect of the plumage was quickly lost by abrasion, but the uniform wear of the outer primaries permitted identification up to 12 months of age. The pattern of moult for the first 12 months was of one wave starting at primary 1 and progressing outward, roughly at one feather per month (Figure 4.1). A regression of date on moult scores for Ospreys less than 12 months old gave an estimated mean date of 1 December for the initiation of the first moult. However, starting dates varied up to 2 months among individuals: estimated from feather growth rates, an Osprey that was caught on 16 December and had already grown one feather would have started to moult in the first half of November; at the other extreme, an Osprey that was caught on 5 February and had not yet finished growing its first primaries would have started in early January.

Nine captures were made of 6 Ospreys, aged between 12 and 31 months, previously ringed as nestlings or yearlings. Three other Ospreys were trapped during the period when breeding birds had returned to Europe. These were aged 21-22 months or older, but since ringing records show that Ospreys have normally returned to

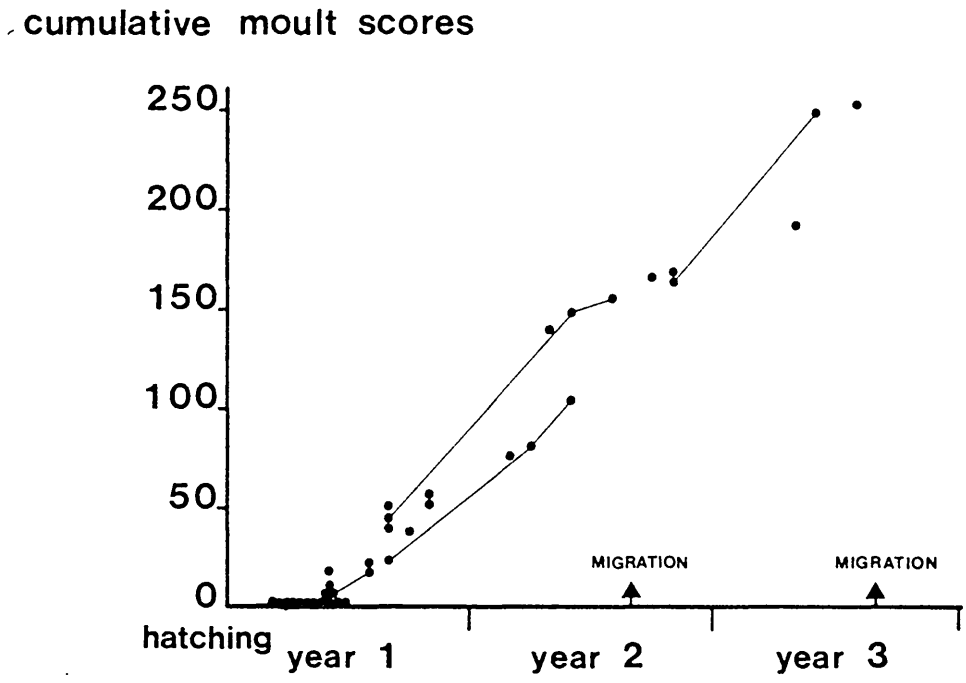

Figure 4.1 Cumulative moult scores of immature Ospreys in Senegambia.

their breeding grounds in Europe by the age of 32 months (Osterlof, 1977), they will be treated as 21-22 months of age. Another bird, trapped at ages 22 and 29 months, probably remained on the wintering grounds in the interim, and on both occasions each wing had only one moult front. Two other individuals caught at ages 28 and 31 months respectively, could have returned to the breeding grounds at age 20 months; both birds had two active moult fronts on each wing. Only one other of the nine Ospreys just mentionned had two moult fronts in its primaries; fronts at primaries 1 and 8 at age 15 months had moved to primaries 2 and 9 at age 17 months; however, once the first moult wave had passed primaries 10, moult would have returned to the single front pattern observed in the other immatures of less than 24 months.

Since all Ospreys in Figure 4.1 were growing primaries, moult was uninterrupted from the moment the first was shed, i.e. from age 5-7 months until age 22 months and even 29 months in one bird. It took about a year to replace the first set of primaries (score of 100 in Figure 4.1) and there was little overlap in time between the first and second waves. The second set of primaries (score of 200 in Figure 4.1) was replaced a little over two years after the start of moult in the first wave; by that time the third wave had already started and there was considerable overlap between the second and third waves.

Three Ospreys ringed as nestlings and caught at age 3 or 4 years had two or three moult fronts in each wing and showed

discontinuities in the sequence of moult; 1 or 2 feathers had been replaced in each wave since the interruption. These birds could be expected to have returned to their breeding grounds in the previous summer and the discontinuities corresponded to an interruption of moult at that time. Three other Ospreys thought to be adults were caught in two successive field seasons. When first caught in February-March 1979, two birds had no growing or missing feathers, but when recaptured in October-December 1979, both had resumed moult at the primaries following the freshest feathers in February-March. The third Osprey was first caught in March 1979 when only primary 7 of each wing had not been renewed and moult had stopped. By February 1980, moult had resumed from primaries 1, 3 and 7 on both wings and all feathers had been renewed; however, L7, older than the other primaries, might have been shed on the breeding grounds.

The results of the examination of skins from the breeding grounds were similar for the two subspecies, P. h. haliaetus and P. h. carolinensis, and are pooled in Table 4.1. Few Ospreys were found moulting between March and July (10%), but 43% of Ospreys collected between July and September were moulting primaries. There was no significant difference between the sexes (chi-square= 3.296, df=1, $p>0.05$). The number of moulting primaries was low: only one primary per wing was missing or growing in 11 Ospreys, two primaries in 4 birds. Moulting of primaries was not restricted to non-breeding birds and one female, BMNH specimen 1931 4844, had two active fronts in each wing while incubating.

month	males		females	
	moulting	not moulting	moulting	not moulting
March	0	1	0	1
April	0	9	2	14
May	1	13	1	5
June	1	1	0	2
July	1	3	3	1
August	2	1	2	2
September	1	1	1	5
October	0	0	0	2
TOTAL	6	29	9	32

Table 4.1. Incidence of moult of primaries among Pandion haliaetus carolinensis and Pandion h. haliaetus on the breeding grounds of North America and Eurasia. Data from skins examined at the American Museum of Natural History in New York, the Smithsonian Institution in Washington, the British Museum (Natural History) in Tring, and the National Museum of Natural Sciences in Ottawa.

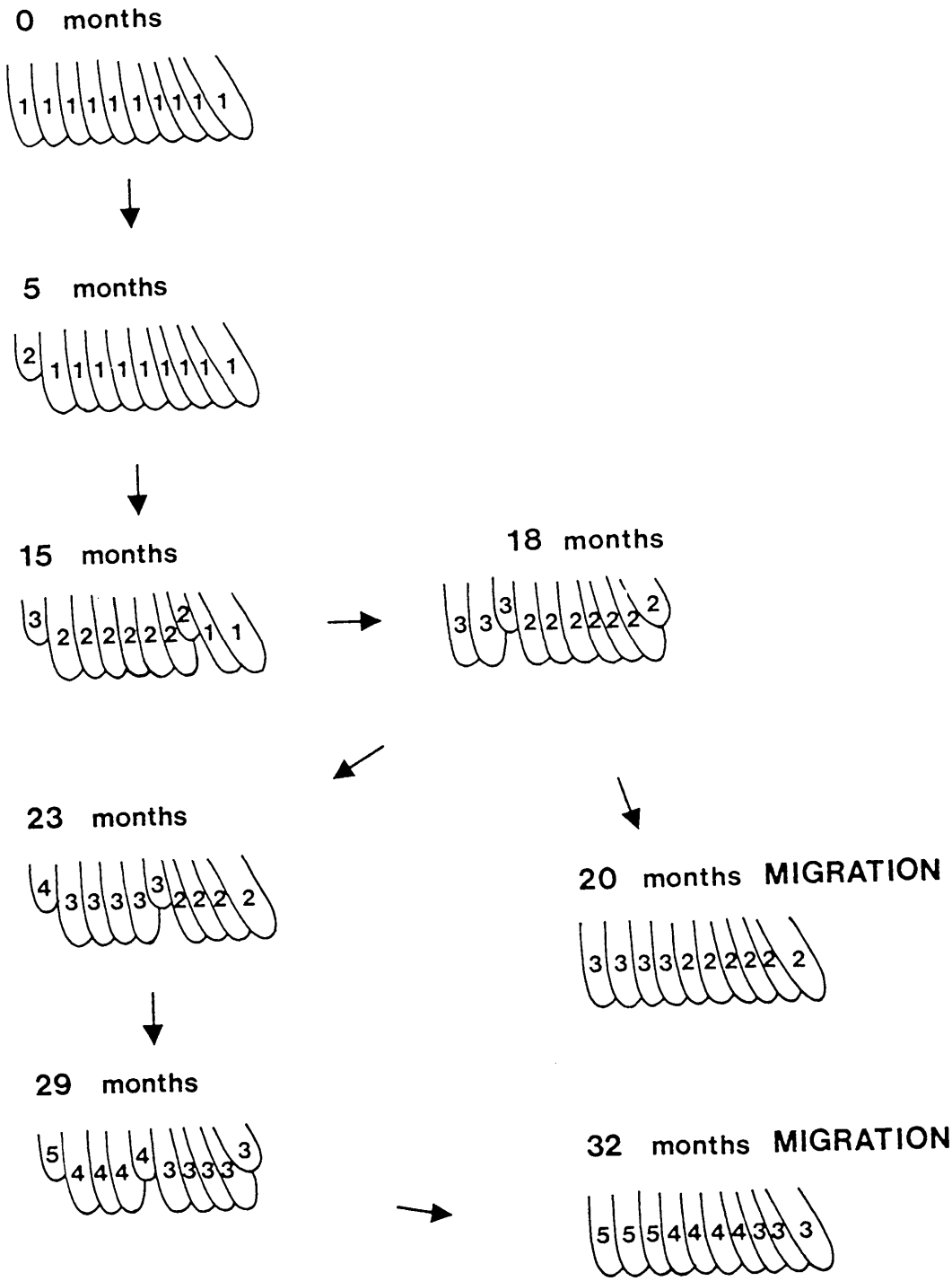

Figure 4.2 The moult pattern of primaries in immature Ospreys. The inner primaries are on the left hand side of each of the wings. Numbers correspond to the wave number, number 1 being the feathers at fledging.

In comparison, 98% of the non yearling Ospreys caught in Senegambia from September to early February were moulting; twelve other Ospreys caught in late February-March, just before spring migration, had stopped moulting after having undergone a complete or nearly complete moult of the primaries.

The preceding data imply that in immature birds primary moult was continuous from initiation until the first return migration to the breeding grounds. Thus for birds returning at age 20 months at least one complete moult will have taken place, and for birds aged 32 months at least two complete moults (Figure 4.2). However, primary moult was interrupted before spring migration to the breeding grounds, but restarted later so that between July and September, nearly half the Ospreys on the breeding grounds were replacing one or two primaries in each wing. Upon return to the wintering grounds moult started again with the feathers distal to the last ones shed. The number of feathers between successive waves was less in mature Ospreys of breeding age than in immatures, causing in mature Ospreys a greater degree of overlap in time of successive moult waves.

4.3.2 ADULTS OF UNKNOWN AGE

The above was worked out in Ospreys of known age. It enabled me to consider as adults Ospreys with two or more moult fronts per wing and with discontinuities in the pattern of wear indicating that moult had been interrupted. Other Ospreys were considered as

immatures. These criteria were unambiguous early in winter, but in February-March, when most primaries had been renewed, discontinuities in one wave could have been erased by the progression of the following wave, so that adults and immatures were not distinguishable. When scoring moult for the current moulting season, I scored only feathers with intact edges and growing feathers (wear scores of 0, 1 or 2).

Figure 4.3 shows moult scores within the winter moulting period for 39 adult Ospreys, plus one recapture, from September to December. A regression of dates on moult scores gave an estimated mean date of 15 October for the start of the moult; however, moult was not synchronous within the population: for example one bird had a score of 74 on 5 December while another had a score of only 30 on 19 December. I used the number of growing or missing primaries in both wings as a measure of moult intensity. The number was greatest early in the moulting season (Table 4.2), but had dropped by February, and 8 of 13 Ospreys caught in March had no growing or missing primaries. However, replacement of primaries was not always complete; 4 of the 8 adults had renewed all their primaries, 2 adults retained one worn primary on both wings and the other two adults retained one worn primary on one wing only.

Only 83% of the moult fronts in adult Ospreys were actively moulting (Table 4.3). In half the cases, 20 of 39 birds, the positions of growing feathers were identical in the two wings, but 9 adults had one less wave in one wing than in the other; some adults

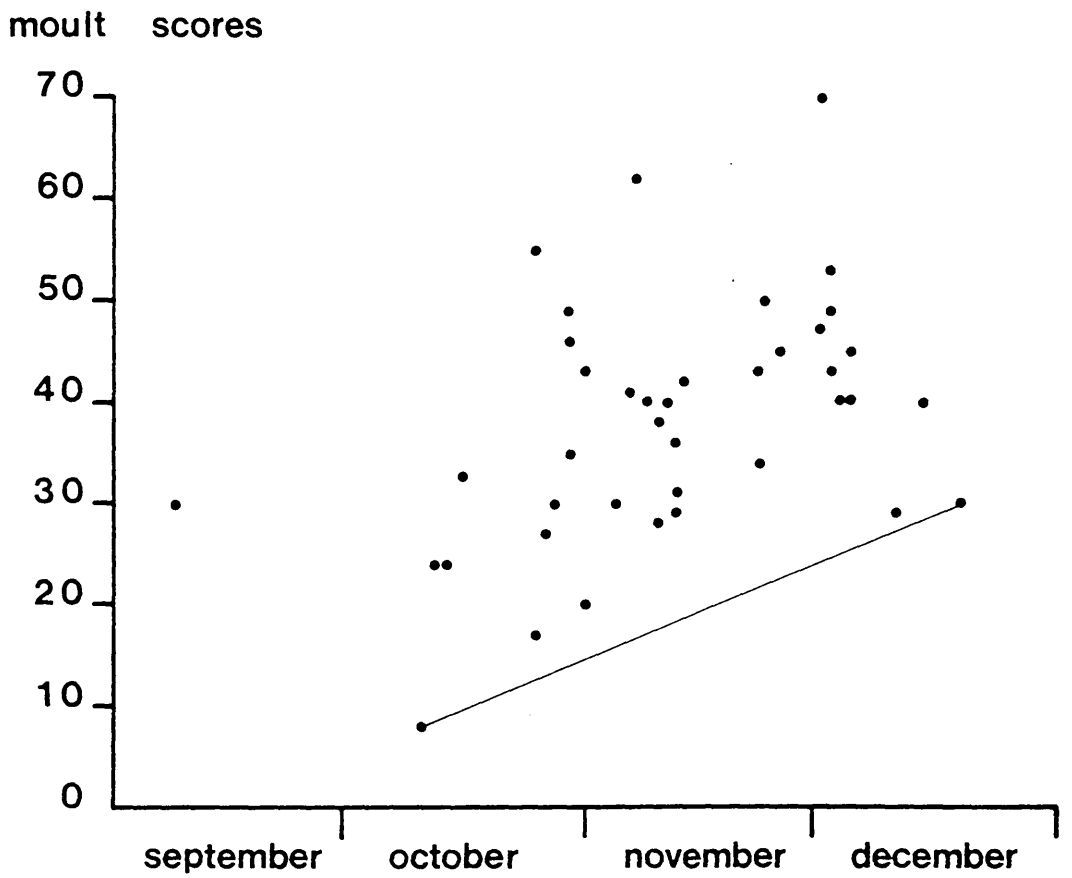

Figure 4.3 Moult scores of adult Ospreys in Senegambia.

month	number of birds examined	mean number of feathers growing or missing (range in brackets)		
		primaries	secondaries	rectrices
September	1	3	1	1
October	13	4.6 (2-8)	6.2 (0-12)	3.8 (1-5)
November	15	4.8 (2-7)	8.2 (6-11)	4.3 (1-6)
December	11	5.1 (3-8)	8.3 (3-16)	4.1 (1-6)
January	-	-	-	-
February	16	2.5 (0-4)	4.2 (1-10)	1.4 (0-3)
March	13	1.0 (0-4)	1.5 (0-3)	0.5 (0-3)

Table 4.2. Number of primaries, secondaries and rectrices growing or missing in Ospreys classed as adults in Senegambia. Moulting feathers from both wings are added for the primaries and secondaries. Secondaries were examined for only 12 Ospreys in February and 6 in March.

number of fronts	number of adults	percentage which had N active fronts					
		1-1	1-2	2-2	2-3	3-3	3-4
2-2	15	27	27	46	-	-	-
2-3	7	-	29	42	29	-	-
3-3	12	-	-	25	17	58	-
3-4	2	-	-	-	-	-	-
4-4	3	-	-	33	-	33	33

Table 4.3. Number of adult Ospreys with different numbers of moult fronts, both active and dormant, and percentage of these Ospreys that had different numbers of active fronts in Senegambia in September-December (sample size is 39). 1-2 means that one wing had one moult front and the other two fronts.

number of waves in each wing	wave number			
	first	second	third	fourth
2	7.3 (6-9)	2.5 (1-5)		
3	8.7 (7-10)	4.9 (3-7)	1.2 (1-3)	
4	8.7 (8-9)	6.6 (6-7)	3.6 (3-4)	1.1 (1-2)

Table 4.4. Average positions in the primaries at which moult started in the wing (range of values in brackets) among adult Ospreys in Senegambia between September and December. The waves are counted from the outer primaries, the first being the outermost.

age class	stage of growth of primary			number of moult fronts examined
	<1/2	1/2-3/4	>3/4	
Immatures (< 12 months)	57%	0%	50%	15
Immatures (> 12 months)	0%	0%	33%	29
Adults	0%	0%	28%	171

Table 4.5. Relationship between the age of Ospreys and the proportion of primaries at different stages of growth where the subsequent primary was missing.

had both dormant and active moult fronts in one wing, showing that these moult waves were out of phase. Moult waves became active at any point of the wing, and the waves were regularly spaced (Table 4.4).

The growth of adjacent primaries, especially the inner ones, frequently overlapped in Ospreys of less than 12 months old. However, for immatures older than 12 months and for adults there was little overlap: the next primary in a wave dropped only after its predecessor had reached 80% or more of its final length (Table 4.5). In some Ospreys there was even a pause, a "negative overlap", between the growth of adjacent primaries. For the most part, therefore, the growing primaries of Ospreys older than 12 months were separated from each other by several complete feathers.

4.3.3 MOULT OF THE SECONDARIES

As for the primaries, secondaries grown before and after migration to Africa could be unambiguously separated until December but not afterwards.

Moult of the secondaries started at age 6-9 months, 1 to 3 months after the start of primary moult. It started from secondaries 1 and 5, progressing in towards the body, and also from the innermost secondary, progressing outwards, a pattern related to the diastataxic break in the region of the fifth secondary where two separate embryonic rows join to make the definitive series of secondaries (Miller, 1941). However, this pattern was lost within a

few months, after which little pattern was discernible, and even symmetry between wings was lost. Secondary moult was continuous until the first return migration to the breeding grounds at age 20 or 32 months; the secondaries had been completely replaced by age 17-19 months, at a cumulative primary score of 150.

Although all adults were moulting secondaries on the wintering grounds, the regression of date on secondary moult scores was not significant ($r=0.26$, $p>0.05$, $df=39$), nor were secondary moult scores significantly correlated with primary or tail moult scores. Secondary moult was probably not as restricted to the wintering grounds as was primary moult, but this was not verified. The growth of adjacent secondaries frequently overlapped, and up to 16 out of the 36 secondaries examined on each bird were missing or growing at one time (Table 4.2).

4.3.4 MOULT OF THE TAIL

Moult of the tail feathers started at age 5-7 months, at primary scores of 5 to 20. It was continuous until the first spring migration, and replacement of the tail was complete by age 14 months, slightly before all primaries had been replaced. Moult started with the innermost rectrices, the fresh central tail feathers contrasting strongly with the others, by then well worn. It progressed outward in each half of the tail, but this pattern was quickly lost, and by the age of 12 months no symmetry remained. Similarly there was no obvious left-right symmetry in the tail moult

of any of the 37 adults caught between September and December.

The regression of date on tail moult scores of adults gave an estimated mean date of 21 October for the start of tail moult. Tail moult had stopped in 10 of 13 Ospreys caught in March (Table 4.2) Tail moult was well correlated with primary moult ($r=0.56$, $p<0.01$, $df=39$), implying a consistent and close relationship between moult in these two tracts.

4.3.5 GROWTH RATE OF INDIVIDUAL FEATHERS

The rate of growth for primaries of 5 Ospreys retrapped within short periods was 5-10.7 mm/day with an overall average of 5.7 mm/day (Table 4.6). However, two primaries of Bird 4, only 1/5 grown, did not grow in the 4 days between captures. This interruption of moult might have resulted from the shock of capture, and it is possible that other birds were similarly affected if interruptions lasted fewer days than the interval between captures.

Daily growth rates of secondaries (average 3.1 mm per day) and rectrices (average 3.2 mm per day) were lower than those of primaries.

	bird 1	bird 2	bird 3	bird 4	bird 5
interval between captures	4 days	3 days	4 days	4 days	3 days
primaries	6.0	5.0	5.0	0.0	6.3
	6.3	9.0	5.0	0.0	
		9.6	6.3	5.5	
		10.7	6.5		
			8.0		
secondaries			1.3	1.7	4.4
			3.0		
			5.2		
rectrices			2.3	2.8	
			2.5	3.0	
			3.7	3.3	
			3.7	3.3	
			4.0		

Table 4.6. Average growth rates (mm per day) of individual feathers of five Ospreys in Senegambia.

4.5 DISCUSSION

4.5.1 THE STAFFELMAUSER IN THE OSPREY

In the Osprey the moult of the primaries occurs in successive waves, each starting at primary 1 and finishing at primary 10; if the moult is interrupted, it resumes from the points where it left off; a new wave starts before the preceding wave reaches primary 10; the number of primaries between successive waves is less in adults than in immatures, so that adults have up to 3 or 4 fronts per wing. Without this pattern of moult, the Staffelmauser (Stresemann, 1966) or continuous stepwise moult (Ashmole, 1968), Ospreys would require more than one year of uninterrupted moult to renew all their primaries if overlap between the growth of adjacent primaries and their growth rates remained the same; however, with the Staffelmauser, all the primaries can be renewed annually.

4.5.2 THE EVOLUTION OF THE STAFFELMAUSER

In species with a single, regular, sequence of moult proceeding outwards from the innermost primary, the rate of moult is controlled by two factors: the rate of growth of individual primaries and the number growing at once (Newton, 1966; Voitkevitch, 1966; Snow, 1976).

In different kinds of birds, the cells producing feathers are basically the same, and their structure is independent of the size of the bird. The rate of feather growth must at some point be

limited by rates of cell division, and this limit may well be similar for all species. This limit might not be reached in species with low levels of certain amino acids, especially cystine and cysteine, in their diets (Newton, 1966, 1968; Dolnik and Gavrilov, 1979). However, growth rates limited by cell division are probably reached in Anseriformes, in order to enable the birds to recover "the power and safety of flight in the shortest time period" (Hanson and Jones, 1976).

The slopes of regressions of wing length on feather growth rates for Passeriformes and Anseriformes, the two orders with large enough sample sizes, were significantly less than that for all orders (Figure 4.4; Table 4.7). This observation fits into the general pattern in biology that regressions of body size on size dependent variables have shallower slopes for lower taxonomic orders (Gould, 1966; Clutton-Brock, 1979). In the case of feather growth, it suggests that growth rates depend more on lifestyle and phylogeny of a bird species than on wing length _per se_.

Although growth rate increases with wing length it is far from being proportional to wing length: longer primaries grow at a relatively much slower rate in relation to their total length. No species, even the largest, have growth rates much above 10 mm/day, while some of the smallest species have growth rates between 4 and 5 mm/day. The narrow range of values casts doubts on the statement by Pienkowski _et al_. (1976) that "interspecific variations in moulting rate are (again) due largely to differences in the growth rates of

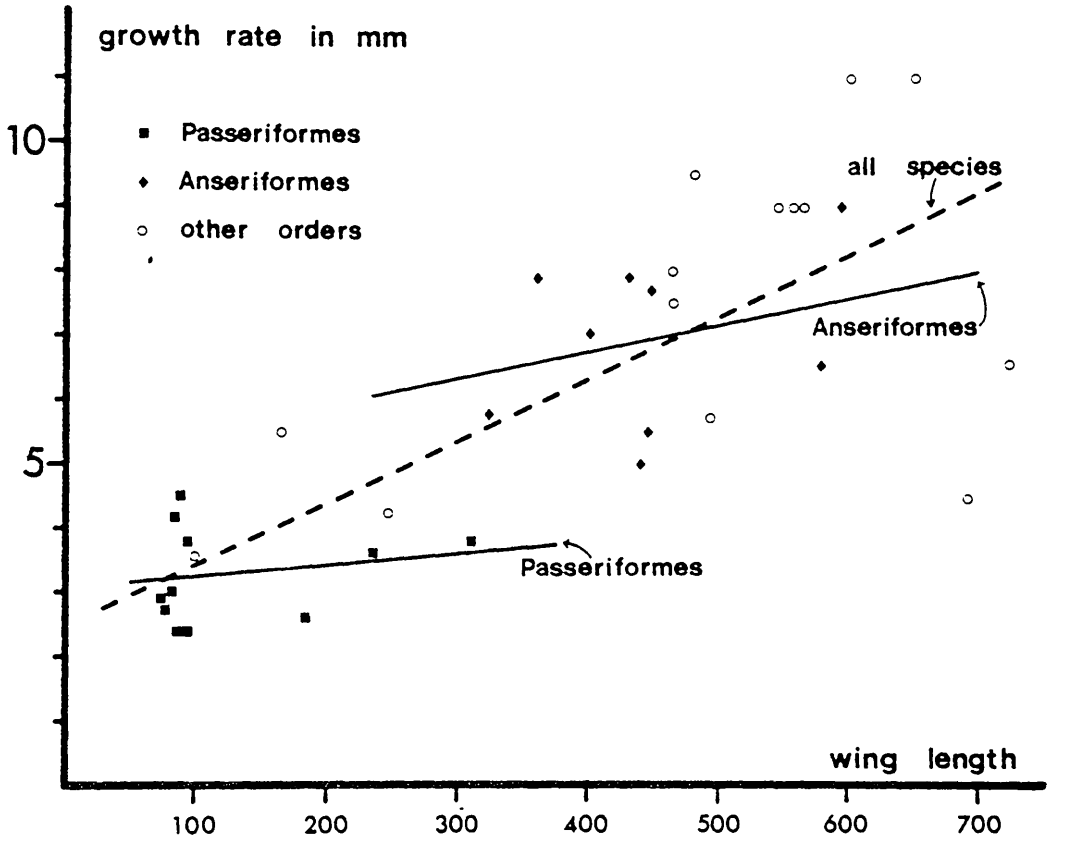

Figure 4.4 Growth rates of feathers in birds versus wing length.

species	daily growth rate in mm	wing length in mm	source
PASSERINES			
Carduelis flammea	2.6-3.2	69-78	Newton, 1969
Passer domesticus	2.6-2.7	71-81	Zeidler, 1966
Carpodacus mexicanus	2.2-3.7	75-83	Michener, 1936
Luscinia luscinia	4.2	78-89	Berger, 1967
Motacilla alba	4.5	81-96	Persson, 1977
Carduelis chloris	2.1-2.6	83-90	Newton, 1967
Pyrrhula pyrrhula	2.1-2.7	87-98	Newton, 1967
Oenanthe oenanthe	3.0-4.5	89-98	Williamson, 1957
Pica pica	1.8-3.4	173-200	Seel, 1976
Corvus monedula	2.8-4.3	225-246	Seel, 1976
Corvus frugilegus	2.7-4.9	290-330	Seel, 1976
ANSERIFORMES			
Branta bernicla	3.8-7.8	296-351	Boyd et al., 1980
Anser rossii	7.9	338-386	Hanson, 1976
Anser caerulescens	7.7-8.0	380-485	Hanson, 1976
Branta leucopsis	7.0-7.6	385-420	Owen et al., 1980
Coscoroba coscoroba	5.0	400-484	Heinroth, 1906
Anser anser	5.5	416-482	Boyd et al., 1980
Branta canadensis interior	6.8-8.7	427-473	Hanson, 1976
Cygnus olor	5.5-8.3	535-622	Mathiasson, 1973
Cygnus cygnus	9.0	562-628	Heinroth, 1906

(continued on next page)

Table 4.7. Average daily growth rates of primaries and wing lengths for various bird species.
Wing lengths are from Witherby (1938) except:
(1) Gypaetus barbatus, Gyps africanus, Streptopelia Streptopelia roseogrisea, and Halcyon leucocephala from Mackworth-Praed and Grant (1952);
(2) Branta bernicla, Branta canadensis, Anser rossii, Anser caerulescens, Meleagris gallopavo and Carpodacus mexicanus from Godfrey (1966);
(3) Oceanodroma homochroa from Palmer (1962);
(4) Coscoroba coscoroba from Blake (1977).
(5) Grus grus, Grus vipio (Pseudogeranus leucochen in Heinroth, 1906), Grus japonensis, Grus leucogeranus, and Bugeranus carunculatus from Walkinshaw (1973). Growth rate for Halcyon leucocephala from P. Jones, pers. comm..

Growth rates were determined from captive birds except for those rates followed by an asterisk in which cases they were determined from wild birds.

species	daily growth rate in mm	wing length in mm	source
OTHER SPECIES			
Halcyon leucocephala	3.6	97-105	Jones, 1980
Oceanodroma homochroa	1.4-2.0	134-148	Ainley, 1976
Streptopelia roseogrisea	5-6	156-171	Riddle, 1908
Phasianus colchicus	5.0-7.2	210-260	Sutter, 1971
Falco tinnunculus	3.8-4.6	230-267	Piechocki, 1956
Meleagris gallopavo	7.5	382-550	Schorger, 1966
Larus hyperboreus	6.0-10.0	440-490	Ingolfsson, 1970
Pandion haliaetus	5.0-10.7	450-540	This study
Larus marinus	7.0-12.0	457-510	Ingolfsson, 1970
Grus grus	9.0	507-608	Stresemann, 1966
Grus vipio	9.0	510-585	Heinroth, 1906
Grus leucogeranus	9.0	538-625	Heinroth, 1906
Grus japonensis	11.0	557-670	Heinroth, 1906
Bugeranus carunculatus	9.0-13.0	613-717	Heinroth, 1906
Gyps africanus	4.4	660-725	Houston, 1975
Gypaetus barbatus	6.6	695-756	Cramp *et al.*, 1980
Gallus gallus	4.0		Riddle, 1908
Coturnix coturnix (juv.)	4.3-4.7		Summers, 1972

Table 4.7. (contd.).

primaries", rather than by variation in the number of primaries growing simultaneously (Morrison, 1976).

The number of simultaneously growing primaries is partly related to the importance of flight in the life of the species (Heinroth, 1931). Complete simultaneous moult causes flightlessness (Woolfenden, 1967), and even an incomplete simultaneous moult can seriously impair flying abilities (Haukioja, 1971; Gaston, 1976; Rohwer and Butler, 1977). Thus Swifts, Apus apus, which depend on their flying skills to feed, show almost no overlap in the growth of adjacent primaries (DeRoo, 1966) and have a prolonged period of primary moult. Nevertheless, because of their small size, moult of the primaries can usually be completed within a single year (DeRoo, 1966). Hirundo rustica, ecologically similar to Swifts, also have a prolonged moult of the primaries with little overlap (Debont, 1962). In comparison, small passerines which depend less on flight, grow several adjacent primaries simultaneously, and replace the whole series in about two months (e.g. Newton, 1966; Snow, 1967).

According to Stresemann (1966), the continuous Staffelmauser, "Kontinuierliche Staffelmauser", is shared by the adults of species in a variety of orders, that have one main feature: large size. Compared to small birds, large birds have high wing loading in spite of disproportionately large wings (Savile, 1957). These species presumably cannot hasten their moult by increasing the growth rate, nor can they increase the overlap in the growth of adjacent primaries without seriously impairing their flying abilities. The

period for a regular outward progressing moult therefore exceeds the period available within the annual cycle. However, some of these species can quicken the replacement of their primaries by changing their moult pattern. Ashmole (1968) and Stresemann (1960) suggested that it is aerodynamically better to moult single primaries simultaneously at several different points of the wing than to moult the same number of primaries in a contiguous group, because the gaps left by single missing primaries will be nearly covered by adjacent ones, a point also made by Bloesch *et al.* (1977) for the White Stork. This is achieved by shortening the interval between moult waves, so that a wave begins before the previous one has finished; the regular outward progressing moult, thought to be the primitive pattern (Stresemann, 1960), is thus modified into the Staffelmauser. In theory up to five waves could occur at once, moulting feathers alternating with complete ones. Nevertheless even the Staffelmauser could seriously impair the flying abilities of very large species with high wing loading; in such a case, reinforcement of the feathers to resist wear over a replacement period of more than one year, seems the only option left.

4.5.3 THE STAFFELMAUSER IN FALCONIFORMES

Stresemann (1960) listed 26 genera of Falconiformes found to have an "irregular" primary moult, with two or more primaries moulting at the same time at different positions along the wing. No genera of Falconidae has a regular outward progressing moult; their moult is

wing length in mm	regular moult (%)	irregular moult (%)
100-200	25 (96)	1 (4)
200-300	37 (80)	8 (20)
300-400	30 (42)	42 (58)
400-500	9 (28)	23 (72)
>500	0 (0)	39 (100)

Table 4.8. Number and percentages of Accipitridae species of different wing-lengths which have an "irregular" moult. Genera with irregular moults are according to Stresemann (1960). Species are from Brown and Amadon (1968). Wing lengths are also from Brown and Amadon (1968) and are an average of male and female wing lengths for each species.

in two waves: one wave progressing inward from primary 4 and the other progressing outward from primary 5 (Piechocki, 1956; Stresemann, 1960). Sagittarius, Pandion and the Cathartid vultures, all of them large birds, have "irregular" moults. Among the Accipitridae there is a clear correlation between the incidence of "irregular" moult and wing length (Table 4.8): all species with an average wing length over 500 mm have an "irregular" primary moult while only one with a wing shorter than 200 mm has such a moult. The smaller species have regular primary moults as described by Newton and Marquiss (1982) for the European Sparrowhawk, Accipiter nisus.

Whenever investigated (e.g. see Cramp and Simmons, 1980), the irregular primary moults were found to be continuous Staffelmauser, such as described for the Osprey in this paper and by Edelstam (1969).

In only a few large Falconiformes has it been determined whether the primaries are all replaced annually by the Staffelmauser or whether the replacement period is longer (Table 4.9). Some of these findings are based on museum specimens or captive birds and will have to be confirmed in the field. Two old world vultures, the Hooded Vulture, Necrosyrtes monachus, and the Egyptian Vulture, Neophron percnopterus, similar to Ospreys in size and wing loading, replace their primaries yearly (Cramp and Simmons, 1980). Jollie (1947) and Spofford (1946) suggested that Golden Eagles, Aquila chrysaetos, require at least two years to replace their primaries.

species	wing length in mm	wing loading N/m sq.	frequency of replacement	source
Pandion haliaetus	450-510	51-65	annual	This study
Necrosyrtes monachus	455-490	49	annual	Cramp et al., 1980
Neophron percnopterus	460-530	45-60	annual	Cramp et al., 1980
Gyps africanus	550-600	77	2-3 years	Houston, 1975
Aquila chrysaetos	570-720	67	1-2 years	Jollie, 1947
Gyps ruepellii	612-665	90	2-3 years	Houston, 1975
Gypaetus barbatus	715-915	56	1-2 years	Cramp et al., 1980
Gymnogyps californianus	807-905	104	2-3 years	Todd et al., 1970

Table 4.9. Wing length, wing loading and frequency of replacement of the primaries in some species of large Falconiformes. wing lengths are from Brown and Amadon (1968); wing wing loadings are also from Brown and Amadon except Gyps africanus and G. rueppellii from Pennycuik (1972).

Jollie's conclusions were based on observations of a captive eagle up to the age of two and a half years. However, the gradual increase in the number of moult fronts with age should have resulted in a nearly complete replacement of all primaries in the following moulting period, which is confirmed by the pattern of wear of adults in Museum collections and contradicts Jollie (1947) and Spofford (1946). Brooke et al. (1972) reported that a complete replacement of the primaries takes nearly two years in Aquila nipalensis and A. pomarina. Jollie (1947) implied that Crandall (1941) had reported an annual replacement of flight feathers in the Bald Eagle, Haliaeetus leucocephalus, but Crandall only discussed rectrices and did not mention remiges; however, Jollie, from his own examination of Museum skins, concluded that Bald Eagles undergo a complete annual replacement.

Although the Lammergeier, Gypaetus barbatus, has very long wings, its low wing loading permits three simultaneous moult fronts per wing (Cramp and Simmons, 1980) and an annual (Menzbier, 1894) or near annual (Cramp and Simmons, 1980) replacement of the primaries. This is clearly not the case in large vultures with higher wing loadings, such as the White-backed Vulture, Gyps africanus, and Ruppell's Vulture, G. rueppellii, where replacement exceeds two years, with only one or two simultaneous moult fronts (Houston, 1975). Todd and Gale (1970) reported similar findings for the Califonia Condor, Gymnogyps californianus, which has a very high wing loading and very long wings, the longest primary reaching 690

mm (Miller, 1937); the gaps left by moulting primaries are completely covered by adjacent primaries thus preserving the plane area of the wing where the greatest strain falls, that is, at the tip (Miller, 1937).

To conclude, it seems that in adults annual replacement is the rule in all but the largest species, and that the extent of annual replacement is inversely related to wing loading. However, there are still few data on the varying intensity of Staffelmauser in large Falconiformes and other large birds.

CHAPTER 5

DISCUSSION: WHY DO OSPREYS NOT BREED IN THE TROPICS?

5.1 INTRODUCTION

The initial question on why Ospreys do not breed in the tropics can be divided into three questions:

- Why have Holarctic migrants not stayed to breed in their tropical wintering grounds?
- Why have Holarctic residents not spread south into the tropics?
- Why have Australasian Ospreys not dispersed northwest into tropical Asia?

The third question cannot be answered until a field study is done of Australasian Ospreys. Their morphological distinctness from Holarctic Ospreys suggests that they have not faced the same selection pressures. The first two questions I will now discuss.

We saw in Chapter 1 that the paleontological record was of little help in explaining present distribution. In this chapter, I shall assume that present distribution results from causes still operating

now rather than causes only in the past. Since Ospreys show the characteristics of a good colonizing species, namely a widespread distribution including remote islands and a strong flying ability, their absence from the tropics is not caused by an inability to disperse. In the following sections I shall discuss ecological and physiological factors that might prevent Ospreys from breeding in the tropics.

5.2 ARE THE TROPICS HOSPITABLE TO BREEDING OSPREYS?

5.2.1 THE TROPICAL ENVIRONMENT

Although Ospreys are present in the tropics all year, it does not follow that they could breed there. The habitat might be good enough to meet the reduced needs of migrants in winter and subadults throughout the year but not those of breeding Ospreys. This was the initial hypothesis that I examined.

The coast of Senegambia comprises habitats typical of Osprey wintering grounds worldwide. I shall assume Senegambia to be a representative wintering area for Holarctic Ospreys and use the data from Senegambia to discuss four factors important to breeding Ospreys: climate, availability of nest sites, availability of food, and interspecific competition and interference.

5.2.2 CLIMATE

The two major aspects of climate which would affect Osprey reproduction in the tropics are rainfall and temperature. Some of the effect could be on food availability and would reduce foraging efficiency, but in this section I am concerned with the direct effects the above variables can have on eggs and, especially, on nestlings, as Osprey nests are always exposed and experience extremes of rainfall and temperature.

Tropical environments differ from temperate ones in their high temperatures, with less pronounced seasonal cycles of warm and cold. In particular, there is seldom unseasonal cold weather, a major problem for birds breeding at high latitudes. Instead, seasons are related to patterns of rainfall. In Senegambia, the rainy season is from May to November, but varies in duration depending on latitude.

Most large birds, including raptors (Newton, 1979) and waterbirds (Immelmann, 1971) breed during the dry season in the tropics, presumably because that is when food is most abundant. I showed in Chapter 3 that this was not the case in Senegambia: foraging efficiency was as high during the rainy season as during the dry season. However, considerable damage to the nest and its contents could be caused by the strong winds and heavy rains of tropical storms, especially since Osprey nests are so exposed. The African Fish Eagle, Haliaetus vocifer, the raptor with an ecology most similar to that of the Osprey, lays eggs in October-December in Senegambia, just after the rains (de Naurois, 1962); we could expect

Ospreys to do the same if they bred in Senegambia.

Elsewhere, the laying dates of Ospreys are related to latitude. Holarctic Ospreys lay eggs as late as early June in the extreme north (Dementiev and Gladkov, 1951), and as early as October south of the tropic of Cancer (Gallagher and Woodcock, 1980). Populations at intermediate latitudes have intermediate laying dates: for example, the southernmost migratory populations start to lay in April (e.g. Glutz von Blotzheim, 1971), while the resident populations north of the tropic of Cancer start in January-March (Glutz von Blotzheim, 1971; Cheng, 1976; Bouvet and Thibault, 1980) This trend is reversed in the southern Hemisphere: laying dates in Australia are as late as November in the south and as early as July at the tropic of Capricorn (Serventy and Whittell, 1962). Australasian Ospreys between the tropic of Capricorn and the equator lay from May to at least July (Table 5.1).

Laying dates were compared with average daily temperatures throughout the breeding range of Ospreys. Average daily temperatures were used because maximum and minimum daily temperatures were not available for all localities. The northern limit of breeding in Ospreys lies south of the 10 degrees C isotherms for average daily temperatures in June-August, the warmest period in the Northern Hemisphere. The southern limit for Holarctic Ospreys lies north of the 25 degrees C isotherm in December-February, the coldest period in the Northern Hemisphere. This corresponds roughly with 10 degrees N. The only exceptions are

locality	latitude	date	collection
Admiralty Gulf	14 S	6 May	BMNH
Queensland		May	BMNH
Queensland	20 S	16 June	Helsinki
Point Cloates	23 S	2 July	BMNH
Point Cloates	23 S	26 July	BMNH
Point Cloates	23 S	31 July	BMNH
Queensland	17 S	10 August	BMNH
North Queensland	<20 S	16 August	Helsinki

Table 5.1. Dates on which eggs of Ospreys were collected in Australasia north of the tropic of Capricorn. From the British Museum of Natural History and the Zoological Museum of the University, Helsinki.

Red Sea Ospreys which breed in December-February at slightly higher temperatures (Aden: 25-26 degrees C, Djibouti: 25-26 degrees C, Tokara: 24-26 degrees C). Thus Holarctic Ospreys breed in a range of temperatures from 10 to 25 degrees C.

On the other hand Ospreys in northern Australasia breed at localities where the lowest monthly average is 26 degrees C and where at least one monthly average reaches 30 degrees C in any three consecutive months.

The duration of the egg-laying period also varies with latitude as in many other birds (Baker, 1938; Newton, 1979). At high latitudes the warm period is short and laying is fairly synchronous: for example, egg-laying lasts over 8 weeks in Corsica (Bouvet and Thibault, 1980), 4 weeks in southern Sweden (Odsjo and Sondell, 1976), but only 2 to 3 weeks north of the Arctic Circle (Cramp and Simmons, 1980). Near the tropic of Cancer, temperatures are much less seasonal and laying is less synchronous: for example, South Florida Ospreys lay eggs from late November to early March, a period of more than 16 weeks, (Ogden, 1977; see also Henny and Anderson, 1979, for western Mexico). South of the tropic of Cancer breeding seasons should become more synchronous if high temperatures limit breeding. The little evidence available suggests that this is not the case: Ospreys in the Cape Verde Islands (Bannerman and Bannerman, 1968) and in islands of the Red Sea (Smith, 1955; Brown, 1970) have long laying seasons that are not confined to the coldest months.

Thus no evidence exists to show that high temperatures limit Osprey breeding distribution, nor, if it does, to explain why Australasian Ospreys are not subject to the same limitations.

It should also be pointed out that Ospreys do not breed in many areas where average monthly temperatures are below 25 degrees C for three consecutive months. These include West Africa down to Guinea, the Indus and Ganges deltas, Northern Indochina, and Africa and South America south of 10 degrees S.

5.2.3 AVAILABILITY OF NEST SITES

Ospreys nest in a wide variety of situations: on the ground or on large objects near the ground on islands free of predators (Bent, 1937; Kenyon, 1947; Smith, 1955; Serventy and Whittell, 1962); on the top of dead or live trees in the north-temperate zone (Cramp and Simmons, 1980; Bent, 1937); on cliffs or rock pinnacles in the Mediterranean and the Atlantic Islands (Terrasse and Terrasse, 1977; Bannerman, 1963, Bannerman and Bannerman, 1968); on old castles in Scotland (Brown and Waterston, 1962), and on various man made-pylons and other structures (e.g. Henny, 1977). These sites have one feature in common: an all round open view.

In Senegambia Ospreys could not nest on or near the ground because of the abundance of predators. Heim de Balsac (1951) thought they could nest on the cliffs of the Cap-Vert peninsula, as they nest on similar cliffs in the Cape Verde Islands (Bannerman and Bannerman, 1968). More likely, they would nest near the mouths of the Senegal

and Saloum Rivers on dead or dying trees, similar to trees used in North America and Europe, or in mangrove, as they do in South Florida (Ogden, 1977; Szaro, 1977), in Mexico (Sprunt, 1977; Henny and Anderson, 1979), along the coast of the Red Sea (Smith, 1955), and in Australia (Macdonald, 1973). There is no reason to suspect that Ospreys in Senegambia would require different structures for nesting than those used in similar habitats elsewhere.

Although it is difficult to determine whether a particular tree is suitable for nesting, we can compare the opportunities available in two habitats: Ospreys nest in South Florida in a habitat which is strikingly similar to the coast of Senegambia. Such similarities probably include the intensity of nest predation. Also other tree-top nesting raptors, such as Fish Eagles and various Old World vultures, do breed in Senegambia.

It thus seems that a range of suitable nest sites are available in plenty and that nest sites cannot be the factor preventing Ospreys from breeding near good food sources in Senegambia.

5.2.4 AVAILABILITY OF FOOD

If we compare the foraging efficiency of Ospreys on the breeding (Table 5.2) and wintering grounds (Table 5.3), we see that they were similar. Values of foraging efficiency involving trout on the breeding grounds were higher than values in Senegambia, because the economics of trout were dramatically more favourable than those of any other species except carp, Cyprinus carpio: trout had a high

locality	prey species	average weight of fish in grams	average time per capture in minutes	kcals per minute foraging
Nova Scotia (Prevost, 1977)	flounder	90	9.5	3.2
Yellowstone Lake (Swenson, 1978)	trout	250	12.4	11.7
Finland fish farm (Prevost, unpub.)	trout	300	17.4	21.5
South Florida (Poole, 1982)	mullet	190	> 25.8	< 4.3
Long Island (Poole, 1982)	flounder	172	> 17.4	< 3.3

Table 5.2. Foraging efficiency of Ospreys in kcal/minute of hunting. The foraging efficiency is the average calorific content of a fish divided by the average time per capture. The average calorific content of fish is the average of the contents for each prey species. This in turn is the average weight X the net energy per 100 g of fish flesh X % edible portion as presented in Tables 3.14 and 5.4. Data from South Florida and Long Island did not include the time spent hunting by Ospreys that did not catch a fish but other data did.

locality	average weight of fish in grams	average time per capture in minutes	kcals per minute foraging
Coastal sand dunes			
February-March	414	63.1	3.2
November	400	20.1	10.0
Mouth of the Senegal River			
February 1979	335	30.2	5.9
March 1979	321	27.1	6.1
February 1980	296	24.0	6.7
March 1980	331	25.8	6.8
April to August	238	17.5	7.0
October a) clear freshwater	212	12.9	8.5
b) floodwaters	214	20.5	5.7
c) clear seawater	281	23.8	6.1
Mouth of the Saloum River			
March	310	16.5	9.9
October	296	30.0	5.3
Inshore Islands			
February	180	17.0	5.7
March	196	16.4	6.3
November	240	38.5	3.4
Shallow coastal tidewaters			
October	260	18.0	7.5
December	249	16.4	8.0
January	324	19.7	8.6
Mangrove			
April-August	151	27.6	2.8
November	182	17.8	5.3

Table 5.3. Foraging efficiency of Ospreys in Senegambia in kcal per minute of hunting. The foraging efficiency is the average calorific value of a fish divided by the average time per capture. The average calorific value of fish is the average of the values for each prey species. This in turn is the average weight X the net energy per 100 g of fish flesh X % edible portion as presented in Table 3.14. The weight of fish more than 400 g was not set at 400 g as in Table 3.15.

species	protein	lipid	net energy kcal per 100 g	% edible portion
rainbow trout (*Salmo gairdneri*)	22	11.7	178	70
sea and brown trout (*Salmo trutta*)	18.4	3.2	89	65
pike (*Esox* spp.)	18.5	0.5	65	43
perch (*Perca* spp.)	19	0.9	67	33
carp (wild) (*Cyprinus carpio*	18.2	2.1	79	53
carp (fish farm) (*Cyprinus carpio*)	17.0	9.0	137	53
winter flounder (*Pseudopleuronectes americanus*)	17.4	0.8	64	58
flounder (*Platichthys flesus*)	16.8	0.3	58	58
eel (*Anguilla anguilla*)	18.0	17.3	215	55
mullet (*Mugil cephalus*)	19.4	5.5	113	52

Table 5.4. Net energy available for maintenance and locomotion per 100 g of fresh flesh of fish taken by Ospreys. Values for metabolizable energy are 4.2 kcal per g of protein and 9.5 per g of lipid (King and Farner, 1961). Conversion factors from metabolizable energy to net energy available for maintenance and locomotion are 0.78 for protein and 0.95 for lipid (de Groote, 1974). Values for protein and lipid content are from Sidwell *et al.* (1974) for rainbow trout and eel, otherwise from Jacquot and Creach (1950). Edible portions from Waterman (1964) and Bell and Canterbury (1976).

lipid content, high edible fraction (Table 5.4), and were usually caught rapidly. Note that the highest value was from a fish farm in Finland and did not represent a natural situation.

Foraging efficiencies during the breeding season could be determined for three studies not involving trout: coastal estuaries in Nova Scotia and near Long Island where Ospreys fed on Winter Flounder, Pseudopleuronectes americanus, a situation typical along the coast of northeastern North America; and from South Florida where Ospreys fed on mullet, Mugil spp. (Table 5.2). The values of foraging efficiency for South Florida and Long Island were biased upwards because the time spent foraging by birds that later quit was not included in the calculations; this underestimated the time per capture. Nevertheless, the foraging efficiency in the two studies involving flounders had values similar to the lowest found in Senegambia because Pleuronectidae have low lipid content, an average edible portion and small size, which features are not compensated by a low time per capture. The value for South Florida was also lower than most of the values for Senegambia.

Although data on foraging efficiency are not available for other important prey in Europe (pike, Esox spp., perch, Perca spp., and Cyprinidae), and North America (pike, perch and Centrarchidae), the data available on lipid content and edible portion (Table 5.4) suggest that, given reasonable times per capture, the foraging efficiency associated with these species will probably be similar to that with flounders.

Moreau (1972) pointed out an important difference between the Holarctic zone in summer and the tropics: shorter daylength which reduces the time available to meet food requirements. Poole (1982) suggested that for the Ospreys in subtropical South Florida shorter daylength "has been the major evolutionary factor selecting for typical clutch size" which is lower than for north temperate Ospreys breeding in longer days. This statement was based on delivery rates at nests, but should be interpreted with caution because differences in the nutritive values of fish were not considered. In fact the higher foraging efficiency in South Florida (Table 5.2) when nutritive value of fish is taken into account largely compensates for the shorter days.

However, in contrast to Ospreys in Senegambia, Europe (Hakkinen, 1978; Prevost, unpub.) and the Red Sea (Meinertzhagen, 1959), Ospreys in South Florida and Long Island ate the whole fish including the gut, tail and bones (Poole, pers. comm.). This suggests that Ospreys were more hungry at these sites, but experience shows it might be an artifact, and that the use of baskets to collect fish remains as in Chapter 3 would prove otherwise. Since differences in nutritive value between fish depended mainly on the proportion of fish flesh which was fat, and there is almost no fat in the guts, tail and bones, eating the whole fish reduced differences in nutritive value in Table 5.3. But even taking account of this, it was unlikely that the true value for South Florida could be so much lower than the value for Long Island

as to suggest that short days affected reproductive performance.

5.2.5 INTERSPECIFIC COMPETITION AND INTERFERENCE

Throughout their range Ospreys encounter one or other of the Fish Eagles, Haliaeetus spp.. Fish Eagles and Ospreys both eat fish and both nest in similar sites. Theoretically, Fish Eagles could compete with Ospreys over food and nest sites. However, they breeed sympatrically with Ospreys in Asia (H. albicilla, H. leucoryphus), in North America (H. leucocephalus), in Melanesia (H. sanfordi), and in Australia (H. leucogaster), in some cases with nests only a few hundred meters apart (Ogden, 1977); they also bred sympatrically in Europe (H. albicilla) before both eagles and Ospreys were persecuted almost to extinction (Bijleveld, 1974).

In Senegambia, Ospreys and Fish Eagles preferred different habitats and used different hunting techniques: Fish Eagles were restricted to large fish on the surface while Ospreys caught smaller fish up to 1 m below the surface. The prey species were also different, so that resource depression by Fish Eagles should not have affected Ospreys. In addition, although fish are important in the diet of Fish Eagles, carrion, mammals and waterfowl are also taken (Brown, 1980). These types of food were not used by Ospreys.

Fish Eagles are notorious for robbing Ospreys of their fish (H. leucocephalus, Prevost, 1979; H. albicilla, Stjernsberg, pers. comm.; H. leucogaster, Serventy, 1965; H. vocifer, Brown, 1970). Although Ospreys usually flew away whenever a Fish Eagle approached,

in two years of study only one Fish Eagle was seen harassing an Osprey, a much lower frequency than with Bald Eagles, H. leucocephalus, in North America (Prevost, 1979). Even then the cost in time to the Osprey was thought to be negligible.

Other fish eating species in Senegambia included the White Pelican, Pelecanus onocrotalus, the cormorants, Phalacrocorax carbo and P. africanus, the terns, Sterna albifrons, S. hirundo, S. nilotica, S. maxima, S. caspia, and the herons, Ardea cinerea, A. purpurea, A. goliath, and Egretta alba.

These species used habitats and foraging methods completely different from those of Ospreys or even Fish Eagles. It is doubtful that any appreciable competition existed between them and Ospreys. Also similar species occur in other areas where Ospreys breed.

Thus the presence of other fish-eating birds on the wintering grounds was almost certainly not important to Ospreys. It seems that no other bird species are likely to prevent Ospreys from breeding in tropical habitats.

5.3 WHY DO MIGRANTS NOT BREED IN THE TROPICS?

5.3.1 THE INITIAL HYPOTHESIS

> "In all, 183 species of birds regularly migrate, wholly or at least to some extent, from the palearctic region to Africa south of the Sahara for the northern winter; and it is a remarkable fact, the reasons for which are not fully understood, that hardly any of them have been reported as remaining to breed in the south" (Moreau, 1952).

Lack (1954) postulated that "birds migrate from their winter quarters when breeding is, on the average, more successful elsewhere". It was here understood that the main factor affecting breeding was the food supply. Similar arguments were made by MacArthur and Connell (1966) and MacArthur (1972).

In the previous section, I have shown that there is reason to assume that Ospreys would be able to breed successfully in Senegambia, as in Europe and North America, if they attempted to breed. There might be nutritional constraints other than energetic constraints but these have not been studied. Under the above assumptions, and if Senegambia is representative of the tropics, there does not appear to be an ecological barrier to Ospreys breeding in the tropics. In this section, I shall discuss physiological constraints that might be encountered by Ospreys in the tropics.

5.3.2 PHOTOPERIODIC CONTROL OF REPRODUCTION

In north-temperate birds breeding is triggered by increasing daylength in spring (e.g. Lofts and Murton, 1968). In particular this is known for several raptors (Newton, 1979) and it is probably also true of migratory Ospreys.

In contrast, there is little seasonal variation in daylength in the tropics, and in tropical birds other factors, namely rain, temperature or food supply trigger breeding (Immelmann, 1971; Newton, 1979). For example, increasing daylength certainly does not trigger breeding in subtropical Ospreys in South Florida, and on islands of the Red Sea or the Atlantic, since some of these lay their eggs in late November and early December (Ogden, 1977) when daylength is decreasing.

North-temperate migrants wintering in the tropics encounter a variation in daylength much smaller than that which triggers their breeding. Therefore, a first physiological limitation of north-temperate migrants to breeding in the tropics is that the variation in daylength in the tropics is not sufficient to trigger breeding. This control is so rigid that there is yet no evidence in the class Aves of an individual from the north-temperate zone migrating to the tropics (23,7 degrees N to 23,7 degrees S), and breeding there.

5.3.3 OUT OF PHASE BREEDING

However, migrants wintering south of the tropic of Capricorn encounter an increase in daylength six months out of phase, because the photoperiod from October to December south of the tropics corresponds to the period from April to June north of the tropics. Migrants might shift their annual cycle by six months (re-entrainment) and breed on the wintering grounds. I will discuss examples in the next section. Re-entrainment has also been found in non-migratory passerines moved from England to Australia, New Zealand and South Africa (Lofts and Murton, 1968; Brosset, 1977).

The conditions for re-entrainment are not met in tropical Asia, where Ospreys winter near the equator, but they are met in South America and Africa, where Ospreys winter as far south as 35 degrees S. In fact, for Ospreys that breed at 35 degrees N the increase in daylength during winter at 35 degrees S is as marked as the one they encounter while breeding.

Re-entrainment would be most likely to occur in adults that had not bred successfully the previous summer and in subadults; successful adults would have just finished breeding when they arrived on their winter grounds and would be unlikely to breed twice in one year.

5.3.4 THE ESTABLISHMENT OF LONG DISTANCE MIGRANTS

Three species of long distance migrants are known to have bred in their wintering grounds of South Africa but not further north: the White Stork, Ciconia ciconia, the Bee-Eater, Merops apiaster, and the House Martin, Delichon urbica, (Snow, 1978a;I. Sinclair, pers. comm.). Two other species have also been reported, the Osprey (Mackworth-Praed and Grant, 1962), and the Common Sandpiper (Voous, 1959), but the breeding records have been questionned (Snow, 1978b). Snow (1978a) suggested that five other species originally colonized Africa by the establishment of north-temperate migrants: Bittern, Botaurus stellarus, Black Stork, Ciconia nigra, Booted Eagle, Hiraaetus pennatus, Mountain Buzzard, Buteo tachardus, African Marsh Harrier, Circus ranivorus. The distribution of these birds and their European counterparts - in two cases in the same superspecies - stop short either north or south of the Sahara, leaving a large gap between the north-temperate and African populations. Moreover, these distributions include South Africa, which is important to the hypothesis, since it is south of the tropic of Capricorn that re-entrainment is likely to occur.

Appropriately, the breeding seasons in South Africa of the species discussed above are all six months out of phase with their palearctic relatives. Once established in South Africa, some of these species presumably spread north to include part of the tropics, the photoperiodic control of their reproduction gradually decreasing with time.

5.3.5 THE ENDOGENOUS ANNUAL CYCLE

Why have no more migrants established themselves south of the tropics and why have the sporadic breeding attempts, including those of Ospreys, not led to the establishment of permanent breeding populations?

An additional physiological limitation to breeding by migrants on their wintering grounds is that the seasonal activities of temperate birds, breeding, moulting, fattening and migration, are part of a schedule controlled by an endogenous circannual cycle (Gwinner, 1981A). The control of seasonal activities by this cycle is particularly rigid in long distance migrants to ensure the proper timing of activities within a year, including the return migration to the breeding grounds (Gwinner, 1981B). This rigidity could be an insurmountable barrier to breeding on the wintering grounds (an idea attributed to Pitelka by Myers, 1980). The rigidity would result from a physiological insensitivity to long daylength, i.e. a photorefractory period (e.g. Lofts and Murton, 1968; Farner and Lewis, 1971; Immelmann, 1971). In north-temperate migrants insensitivity would extend to phase shifted increases in daylength south of the tropic of Capricorn (see Hamner and Stocking, 1970, for a discussion of photorefractoriness in the Bobolink, Dolichonyx orizivorus).

The first return migration to the breeding ground of immatures in species with delayed maturity is also probably regulated by an endogenous cycle set in motion soon after hatching and extending

until maturity. By analogy with adults, this cycle would be a barrier to breeding in the tropics by immatures before their first return migration.

5.3.6 FACTORS FAVOURING THE ESTABLISHMENT OF MIGRANTS

The examples discussed previously in section 5.3.4. show that the endogenous control of seasonal activities is not absolute. Two factors favouring the establishment of north-temperate migrants as breeders south of the tropic of Capricorn are a high density of wintering birds and deferred maturity: immatures of species with deferred maturity often stay on the wintering grounds until mature.

Although immature European Ospreys stay in Africa for two or three years, too few remain in South Africa for breeding attempts to occur other than rarely: a maximum of 100 to 200 Ospreys winter there along 3000 km of shoreline (I. Sinclair, pers. comm.), including no more than 40-80 immatures. The bulk of European Ospreys winter in tropical Africa (Osterlof, 1977), where daylength changes are less favourable to the establishment of migrants for the reasons mentionned previously. For example, 800 Ospreys winter along the 600 km of coast in Senegambia (Chapter 2).

The situation in the Americas is analogous: banding returns (Henny and Van Velzen, 1972) showed that North American Ospreys winter mostly in Central America and the northern part of South America, and not in southern South America, the area where re-entrainement would occur.

To conclude, migrants Ospreys are unlikely candidates to breed on their wintering grounds because they may be physiologically prevented from doing so over most of their wintering range, and where they are less prevented in this way, they are not abundant enough for breeding to occur other than extremely rarely.

5.4 WHY HAVE OSPREYS NOT SPREAD INTO THE TROPICS?

5.4.1 MIGRANT-RESIDENT EXCLUSION

Dorst (1962) was the first to suggest that birds wintering in the tropics could stop ecologically similar species from breeding. A similar hypothesis has more recently been made for the Scolopacidae in South America. Myers (1980) speculated that intraspecific competition among wintering migrants has prevented any from breeding and has favoured an increase in rigidity of the endogenous annual cycle. The Scolopacidae are a family of mostly arctic birds (Salomonsen, 1972), and apart from snipe, *Capella* spp., and woodcock, *Scolopax* spp., no Scolopacidae breed south of the tropic of Cancer (Heinzel *et al.*, 1972; Robbins *et al.*, 1966). Therefore the establishment of most Scolopacidae in the Southern Hemisphere can only come from north-temperate migrants establishing themselves on the wintering grounds, and not from a gradual expansion of the breeding range into the tropics.

In Ospreys, as in the Scolopacidae, colonists could come from the

establishment of dephased migrants south of the tropic of Capricorn, and Myers' (1980) hypothesis could then apply. However, in view of what I discussed earlier, Ospreys are more likely to colonize by southward dispersal from the populations that straddle the tropic of Cancer. Breeding attempts would be by immatures, and would occur at the zone of contact between wintering migrants and breeding residents. Breeding attempts would be in winter because this is the breeding season of all the resident subtropical populations. Most relevantly for Senegambia, Ospreys in the Cape Verde Islands, at the same latitude as Senegambia (16 degrees N) and only 700 km away, breed in winter.

The distribution of wintering Ospreys and that of resident Ospreys breeding in winter are mutually exclusive both in the Palearctic and in North America (Figure 5.1). I suggest that the area of high density of Ospreys, roughly between the equator and 15 degrees N, acts as a barrier to the southern expansion of resident Ospreys. However, at latitudes below the tropic of Capricorn migrants would be at too low a density to interfere with breeding attempts by other migrants.

The purported interference would be active, such as the attempts to steal fish reported in Chapter 3, rather than insidious, such as competition through resource depression. As an example, if an Osprey tried to breed at the mouth of the Senegal River, it would encounter about 100 wintering Ospreys in an area of 20 to 30 km square. Since it would have to bring fish to a nest site which is

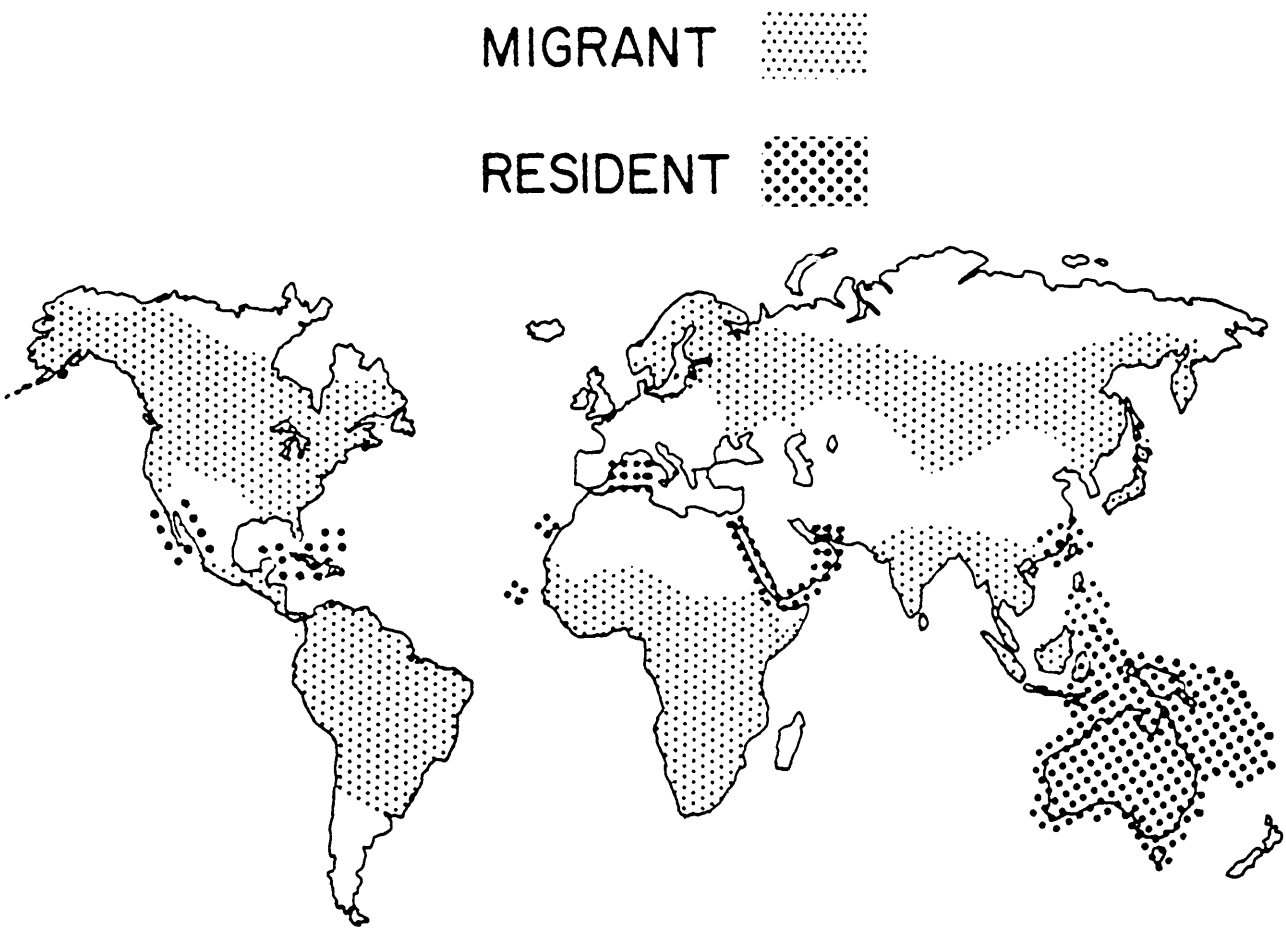

Figure 5.1 Breeding grounds of resident and migrant Ospreys and wintering grounds of migrant Ospreys.

necessarily fixed, it could become the target of perpetual robbery attempts. In contrast, a non-breeding Osprey could avoid most attempts simply by flying away.

Although robbery attempts have been observed on the Holarctic breeding ground (Prevost, unpub.) these were much less frequent than in Senegambia. Robbing is an energetically cheap way to get a fish, but it is not reliable because opportunities in a day are few and unpredictable. These are only minor problems for non-breeding birds, since they catch fish only for themselves and have most of the day to do this. They can afford to perch near a foraging site in wait of an opportunity to rob another bird, and I would expect them to be responsible for most robbery attempts on the breeding grounds. In contrast, breeding birds must bring a larger food supply to the nest within a shorter time. They cannot afford to wait for opportunities to rob another bird and I expect they seldom attempt to do so.

Palearctic Ospreys do not winter in the Cape Verde Islands although they do winter at corresponding latitudes on the continent of Africa. Significantly, Ospreys breed on the Cape Verde Islands, and this is the southernmost breeding population of Holarctic Ospreys.

Shifting of the breeding season to avoid migrants would be countered by the selective forces that restricted breeding to winter in the first place.

5.4.2 WHY DO MIGRANTS LEAP-FROG RESIDENTS?

Ospreys breeding in the north-temperate zone must migrate south because their food becomes unavailable during the northern winter. Natural selection will have favoured those migrants wintering in the most favourable habitat accessible to them, taking into account the cost of migration. Under this hypothesis, the reason why few north-temperate migrants winter north of the tropic of Cancer would be that these habitats (Lower California, Gulf of Mexico, Mediterranean Sea, Red Sea, Persian Gulf and southern China) are less favourable in winter than habitats further south. It follows that the area between the breeding and wintering grounds of migrants is likely to be less favourable for breeding - nevertheless sufficiently favourable for breeding to occur - than habitats further south. Residents can breed there, but not further south, because the few migrants wintering north of the tropic of Cancer do not seriously disturb them. If ever migrants wintered in numbers in these areas, I believe they would in the end evict the residents as they would interfere with the breeding of residents much more than these would interfere with their activities.

APPENDIX 1

A TRAP FOR CATCHING OSPREYS AWAY FROM THE NEST

INTRODUCTION

Female Ospreys (Pandion haliaetus) have regularly been caught with noose carpets at nest sites in North America and Europe (Fernandez and Fernandez 1977; Poole, Postupalsky, Saurola, personal communications). However, males at nest sites and Ospreys away from the nest, such as at a foraging site, on a wintering ground or on migration, have rarely been caught because of a lack of a proper trap. In this note, I will describe a trap which Jock Baker and I developed in 1979 to catch Ospreys on their wintering grounds in Senegambia. It has since been used on the breeding grounds grounds to catch male Ospreys (Poole, pers. comm.; Reitherman and Storrer, pers. comm.).

TRAP DESIGN

The trap (Figure 1) is a snare powered by a thin strip of heavy rubber from an inner tube (3-5 mm wide by 1.4 m long). The inner tube pulls shut a noose of braided nylon (1.0 - 1.5 m long, 2 mm in diameter) held in position by 2 holders made from galvanized steel wire 1.5 mm in diameter (all jagged ends are carefully tucked away). An end guide and a main guide, made of heavier galvanized steel wire 3 mm in diameter, make the noose jump up when it is pulled shut.

The trigger mechanism (Figure 2) is centered about a piece of galvanized steel wire 3 mm in diameter twisted onto itself to form a narrow slit through which is placed a thin plastic washer tied to the line of the noose, itself tied to one end of the strip of inner tube. The other end of the inner tube strip is tied to a post about 3 m from the perch. The tension of the inner tube is maintained by blocking the washer with the end of a 150 pound test monofilament line (Figure 2), and is sufficient to keep the monofilament from slipping out of the washer. The other end of the monofilament is tied to the end guide about 30 cm away from the trigger mechanism (Figure 1). The monofilament is pulled taut and any excess past the wire that holds it is clipped (Figure 3A). For the trap to be sensitive, the monofilament must fit snugly in the washer's hole, the washer must fit snugly in the slit, and the trigger mechanism and end guide must be rigid.

If an Osprey lands it presses down on the monofilament, freeing

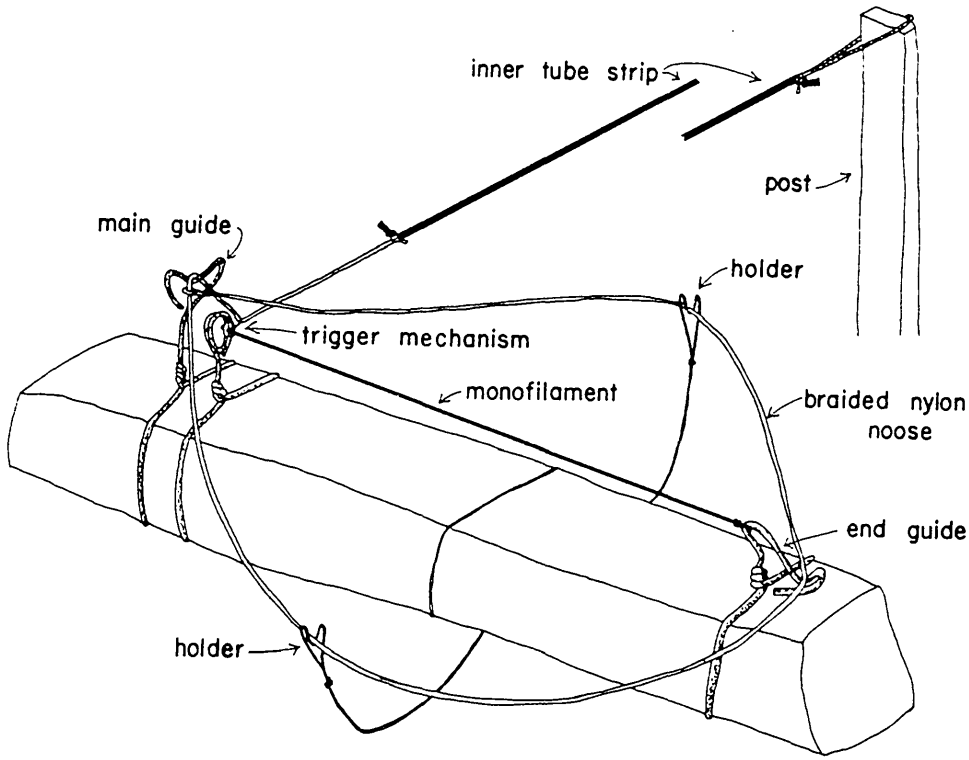

Figure 6.1 A trap for catching Ospreys.

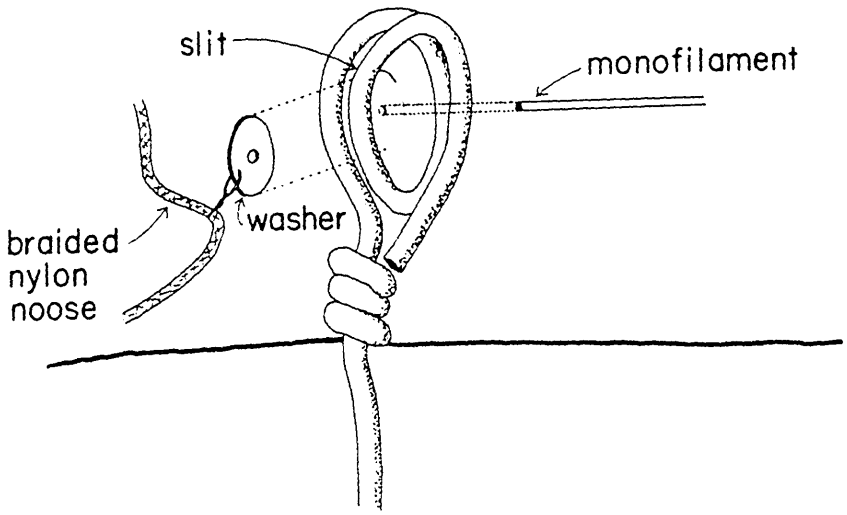

Figure 6.2 The trigger mechanism.

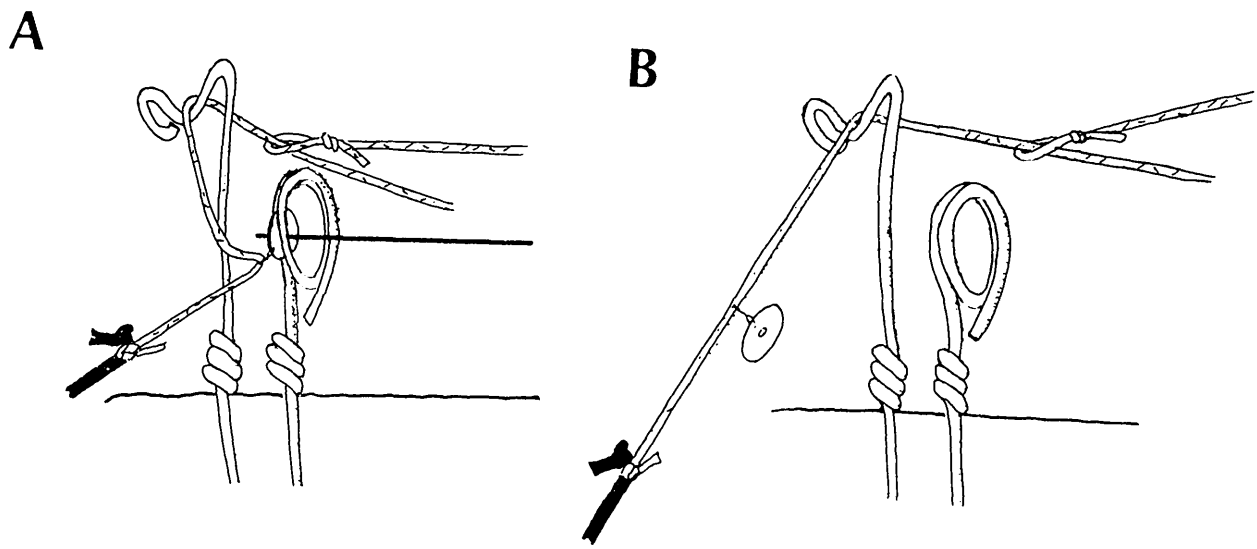

Figure 6.3 The trigger mechanism when the trap is set and when the trap is released.

the washer. The inner tube strip pulls the noose perpendicular to the perch (Figure 3A). The noose is kept from slipping under the Osprey's leg by the main guide, but once it is nearly shut the lateral pull makes the nylon line slip over the main guide. Once caught, the Osprey usually flies off, pulling free the strip of inner tube from the post. A line tied from the noose to the perch tethers the Osprey or better still the line is tied to a drag line or a weight of about 2 kilos.

SAFETY

There is often the threat of injury when trapping animals. Of 149 captures involving 120 different Ospreys, two Ospreys were injured. In both cases there were no external injuries, but the Osprey could not fly properly when released; although offered fresh fish they weakened and died within 3 days in captivity.

In the first case, the tension on the strip of inner tube was so strong that it pulled the Osprey off the perch after the noose had shut. To alleviate this, the strip of inner tube should be narrow. In addition, it should only be stretched enough to pull shut the noose and a little more. Although gentle, the trap will remain quick.

In the second case, before we could get to it the Osprey wound its tether around the perch and trap hitting against them in its

struggle to escape. Thus all traps must be under constant observation when set and be readily accessible to the observer.

SOME TIPS ON TRAPPING

The trap exploits the tendencies of Ospreys to use preferred perches to rest or feed on (Figure 4). The key to successful trapping lays in identifying these perches and limiting their availability by selectively removing perches unsuitable for trapping or installing artificial perches. A high proportion of the population can be caught: in our case about 50% of the Ospreys wintering at the mouth of the Senegal River. In addition, Ospreys do not become trap shy to the point that recapture is impossible: of 120 Ospreys, 17 were captured twice, 4 were captured 3 times and 1 was captured 5 times.

Many traps can be installed, because each is easy to build and inexpensive (no more than 2 US dollars). Contrary to traps of fixed design, such as the Verbail used for Bald Eagles in Alaska (Robarts, 1967), each trap can be adapted to the particular perch. If properly set, its high sensitivity makes it trigger everytime an Osprey lands on it and a carefully made trap will catch almost every time, especially if the noose holders are adjusted for wind direction (since the Osprey invariably lands from downwind, the upwind holders should be higher than the downwind holders). In

Figure 6.4 A typical Osprey feeding perch with a trap set on it.

addition, the trap's ability to pull shut a large noose (over 0.5 m in diameter) makes it highly suited for Ospreys, which frequently land with a fish dangling in their talons.

To conclude, this trap is inexpensive, simple to build and operate and, if used carefully, it is reliable and safe.

APPENDIX 2: DATA ON DIET IN SENEGAMBIA

In the following pages I have included the data on diet which are discussed in Chapter 3. In pages 214-263, I have included tables giving the average estimated lengths and weights of the major fish species caught by Ospreys. The estimates were obtained from opercula as detailed in Chapter 3. The average weight corrected was obtained by setting at 400 g the weight of fish heavier than 400 g.

In pages 264-272, I have included tables giving the percentage frequencies of fish species eaten by ospreys as determined from tails collected at feeding perches. These data are less complete than the data from opercula, but provide a useful comparison. In particular, it is clear that the frequencies of species with soft opercula (see Table 3.1) were underestimated when using opercula.

Coastal sand dunes February-March 1979
Average length and weight of fish estimated from opercula

species	length in mm	weight in g	%	number of opercula	
				all	intact
Liza dumerili	0 +- 0	0 +- 0	0.0	0	0
Liza grandisquammis	0 +- 0	0 +- 0	0.0	0	0
Liza falcipinnis	336 +- 36	453 +-148	8.2	6	5
Mugil curema	0 +- 0	0 +- 0	0.0	0	0
Mugil monodi	0 +- 0	0 +- 0	2.7	2	0
Mugil cephalus	320 +- 97	526 +-389	9.6	7	7
Mugil bananensis	279 +- 3	332 +- 12	6.8	5	3
Ethmalosa dorsalis	270 +- 0	368 +- 0	4.1	3	1
Sardinella aurita	309 +- 0	494 +- 0	1.4	1	1
Sardinella maderensis	236 +- 19	242 +- 73	15.1	11	8
Dicentrarchus punctatus	0 +- 0	0 +- 0	0.0	0	0
Pomadasys spp.	309 +- 59	523 +-251	27.4	20	19
Sarotherodon spp.	0 +- 0	0 +- 0	0.0	0	0
Smaris melanurus	0 +- 0	0 +- 0	0.0	0	0
Cheilopogon heterurus	0 +- 0	0 +- 0	1.4	1	0
Strongylura crocodila	0 +- 0	0 +- 0	8.6	6	0
Galeoides decadactylus	0 +- 0	0 +- 0	4.1	3	0
Mugil spp.	0 +- 0	0 +- 0	4.1	3	0
Liza spp.	0 +- 0	0 +- 0	0.0	0	0
Others	0 +- 0	0 +- 0	5.5	4	0
Pseudotolithus spp.	0 +- 0	0 +- 0	0.0	0	0
Caranx spp.	0 +- 0	0 +- 0	0.0	0	0
Lichia glauca	0 +- 0	0 +- 0	0.0	0	0
Other Carangidae	0 +- 0	0 +- 0	0.0	0	0

Sample size = 73
Average weight = 414
Average corrected weight= 310

Coastal sand dunes June-August 1979
Average length and weight of fish estimated from opercula

species	length in mm	weight in g	%	number of opercula	
				all	intact
Liza dumerili	237 +- 0	159 +- 0	2.2	1	1
Liza grandisquammis	0 +- 0	0 +- 0	0.0	0	0
Liza falcipinnis	249 +- 0	164 +- 0	2.2	1	1
Mugil curema	0 +- 0	0 +- 0	0.0	0	0
Mugil monodi	0 +- 0	0 +- 0	0.0	0	0
Mugil cephalus	0 +- 0	0 +- 0	0.0	0	0
Mugil bananensis	209 +- 24	128 +- 46	6.7	3	3
Ethmalosa dorsalis	0 +- 0	0 +- 0	2.2	1	0
Sardinella aurita	202 +- 13	120 +- 27	11.1	5	4
Sardinella maderensis	227 +- 16	209 +- 53	44.4	20	18
Dicentrarchus punctatus	0 +- 0	0 +- 0	0.0	0	0
Pomadasys spp.	358 +- 46	746 +-243	11.1	5	3
Sarotherodon spp.	0 +- 0	0 +- 0	0.0	0	0
Smaris melanurus	0 +- 0	0 +- 0	0.0	0	0
Cheilopogon heterurus	0 +- 0	0 +- 0	0.0	0	0
Strongylura crocodila	0 +- 0	0 +- 0	0.0	0	0
Galeoides decadactylus	0 +- 0	0 +- 0	0.0	0	0
Mugil spp.	0 +- 0	0 +- 0	0.0	0	0
Liza spp.	0 +- 0	0 +- 0	0.0	0	0
Others	0 +- 0	0 +- 0	2.2	1	0
Pseudotolithus spp.	0 +- 0	0 +- 0	0.0	0	0
Caranx spp.	0 +- 0	0 +- 0	8.9	4	0
Lichia glauca	0 +- 0	0 +- 0	8.9	4	0
Other Carangidae	0 +- 0	0 +- 0	0.0	0	0

Sample size = 45
Average weight = 256
Average corrected weight= 207

Coastal sand dunes November 1979
Average length and weight of fish estimated from opercula

species	length in mm	weight in g	%	number of opercula	
				all	intact
Liza dumerili	0 +- 0	0 +- 0	0.0	0	0
Liza grandisquammis	0 +- 0	0 +- 0	0.0	0	0
Liza falcipinnis	291 +- 67	321 +-250	15.6	5	5
Mugil curema	0 +- 0	0 +- 0	0.0	0	0
Mugil monodi	0 +- 0	0 +- 0	6.3	2	0
Mugil cephalus	0 +- 0	0 +- 0	0.0	0	0
Mugil bananensis	184 +- 0	80 +- 0	3.1	1	1
Ethmalosa dorsalis	0 +- 0	0 +- 0	0.0	0	0
Sardinella aurita	232 +- 7	194 +- 22	6.3	2	2
Sardinella maderensis	213 +- 14	165 +- 39	21.9	7	7
Dicentrarchus punctatus	0 +- 0	0 +- 0	0.0	0	0
Pomadasys spp.	0 +- 0	0 +- 0	0.0	0	0
Sarotherodon spp.	0 +- 0	0 +- 0	0.0	0	0
Smaris melanurus	0 +- 0	0 +- 0	0.0	0	0
Cheilopogon heterurus	0 +- 0	0 +- 0	6.3	2	0
Strongylura crocodila	0 +- 0	0 +- 0	3.1	1	0
Galeoides decadactylus	0 +- 0	0 +- 0	0.0	0	0
Mugil spp.	0 +- 0	0 +- 0	0.0	0	0
Liza spp.	0 +- 0	0 +- 0	0.0	0	0
Others	0 +- 0	0 +- 0	18.8	6	0
Pseudotolithus spp.	0 +- 0	0 +- 0	0.0	0	0
Caranx spp.	0 +- 0	0 +- 0	25.0	8	0
Lichia glauca	0 +- 0	0 +- 0	0.0	0	0
Other Carangidae	0 +- 0	0 +- 0	0.0	0	0

Sample size = 32
Average weight = 215
Average corrected weight= 192

Mouth of the Senegal River February 1979
Average length and weight of fish estimated from opercula

species	length in mm	weight in g	%	number of opercula	
				all	intact
Liza dumerili	0 +- 0	0 +- 0	0.0	0	0
Liza grandisquammis	0 +- 0	0 +- 0	0.0	0	0
Liza falcipinnis	350 +- 36	507 +-163	11.1	3	2
Mugil curema	0 +- 0	0 +- 0	0.0	0	0
Mugil monodi	0 +- 0	0 +- 0	3.7	1	0
Mugil cephalus	283 +- 46	305 +-158	70.4	19	18
Mugil bananensis	0 +- 0	0 +- 0	0.0	0	0
Ethmalosa dorsalis	284 +- 11	433 +- 55	14.8	4	3
Sardinella aurita	0 +- 0	0 +- 0	0.0	0	0
Sardinella maderensis	0 +- 0	0 +- 0	0.0	0	0
Dicentrarchus punctatus	0 +- 0	0 +- 0	0.0	0	0
Pomadasys spp.	0 +- 0	0 +- 0	0.0	0	0
Sarotherodon spp.	0 +- 0	0 +- 0	0.0	0	0
Smaris melanurus	0 +- 0	0 +- 0	0.0	0	0
Cheilopogon heterurus	0 +- 0	0 +- 0	0.0	0	0
Strongylura crocodila	0 +- 0	0 +- 0	0.0	0	0
Galeoides decadactylus	0 +- 0	0 +- 0	0.0	0	0
Mugil spp.	0 +- 0	0 +- 0	0.0	0	0
Liza spp.	0 +- 0	0 +- 0	0.0	0	0
Others	0 +- 0	0 +- 0	0.0	0	0
Pseudotolithus spp.	0 +- 0	0 +- 0	0.0	0	0
Caranx spp.	0 +- 0	0 +- 0	0.0	0	0
Lichia glauca	0 +- 0	0 +- 0	0.0	0	0
Other Carangidae	0 +- 0	0 +- 0	0.0	0	0

Sample size = 27
Average weight = 335
Average corrected weight= 295

Mouth of the Senegal River March 1979
Average length and weight of fish estimated from opercula

species	length in mm	weight in g	%	number of opercula	
				all	intact
Liza dumerili	230 +- 0	144 +- 0	1.3	1	1
Liza grandisquammis	296 +- 0	327 +- 0	1.3	1	1
Liza falcipinnis	340 +- 40	469 +-178	2.6	2	2
Mugil curema	0 +- 0	0 +- 0	0.0	0	0
Mugil monodi	0 +- 0	0 +- 0	0.0	0	0
Mugil cephalus	278 +- 54	304 +-214	75.0	57	56
Mugil bananensis	0 +- 0	0 +- 0	0.0	0	0
Ethmalosa dorsalis	293 +- 12	480 +- 64	3.9	3	3
Sardinella aurita	0 +- 0	0 +- 0	0.0	0	0
Sardinella maderensis	0 +- 0	0 +- 0	0.0	0	0
Dicentrarchus punctatus	0 +- 0	0 +- 0	0.0	0	0
Pomadasys spp.	0 +- 0	0 +- 0	0.0	0	0
Sarotherodon spp.	276 +- 8	387 +- 35	7.9	6	6
Smaris melanurus	0 +- 0	0 +- 0	0.0	0	0
Cheilopogon heterurus	0 +- 0	0 +- 0	0.0	0	0
Strongylura crocodila	0 +- 0	0 +- 0	0.0	0	0
Galeoides decadactylus	0 +- 0	0 +- 0	0.0	0	0
Mugil spp.	0 +- 0	0 +- 0	5.3	4	0
Liza spp.	0 +- 0	0 +- 0	0.0	0	0
Others	0 +- 0	0 +- 0	2.6	2	0
Pseudotolithus spp.	0 +- 0	0 +- 0	0.0	0	0
Caranx spp.	0 +- 0	0 +- 0	0.0	0	0
Lichia glauca	0 +- 0	0 +- 0	0.0	0	0
Other Carangidae	0 +- 0	0 +- 0	0.0	0	0

Sample size = 76
Average weight = 321
Average corrected weight= 267

Mouth of the Senegal River April-August 1979
Average length and weight of fish estimated from opercula

species	length in mm	weight in g	%	number of opercula	
				all	intact
Liza dumerili	226 +- 0	137 +- 0	1.4	1	1
Liza grandisquammis	297 +- 16	332 +- 62	2.8	2	2
Liza falcipinnis	334 +- 0	424 +- 0	2.8	2	1
Mugil curema	0 +- 0	0 +- 0	0.0	0	0
Mugil monodi	0 +- 0	0 +- 0	1.4	1	0
Mugil cephalus	251 +- 49	220 +-184	63.4	45	42
Mugil bananensis	211 +- 37	140 +- 87	7.0	5	4
Ethmalosa dorsalis	260 +- 31	337 +-123	4.2	3	2
Sardinella aurita	0 +- 0	0 +- 0	0.0	0	0
Sardinella maderensis	267 +- 0	365 +- 0	2.8	2	1
Dicentrarchus punctatus	0 +- 0	0 +- 0	0.0	0	0
Pomadasys spp.	310 +- 2	488 +- 10	2.8	2	2
Sarotherodon spp.	238 +- 32	263 +-101	4.2	3	3
Smaris melanurus	0 +- 0	0 +- 0	0.0	0	0
Cheilopogon heterurus	0 +- 0	0 +- 0	0.0	0	0
Strongylura crocodila	0 +- 0	0 +- 0	0.0	0	0
Galeoides decadactylus	0 +- 0	0 +- 0	0.0	0	0
Mugil spp.	0 +- 0	0 +- 0	4.2	3	0
Liza spp.	0 +- 0	0 +- 0	0.0	0	0
Others	0 +- 0	0 +- 0	2.8	2	0
Pseudotolithus spp.	0 +- 0	0 +- 0	0.0	0	0
Caranx spp.	0 +- 0	0 +- 0	0.0	0	0
Lichia glauca	0 +- 0	0 +- 0	0.0	0	0
Other Carangidae	0 +- 0	0 +- 0	0.0	0	0

Sample size = 71
Average weight = 238
Average corrected weight= 212

Mouth of the Senegal River October 1979, clear seawater
Average length and weight of fish estimated from opercula

species	length in mm	weight in g	%	number of opercula	
				all	intact
Liza dumerili	270 +- 94	291 +-275	22.2	2	2
Liza grandisquammis	0 +- 0	0 +- 0	0.0	0	0
Liza falcipinnis	0 +- 0	0 +- 0	0.0	0	0
Mugil curema	0 +- 0	0 +- 0	0.0	0	0
Mugil monodi	0 +- 0	0 +- 0	0.0	0	0
Mugil cephalus	261 +- 84	277 +-265	44.4	4	4
Mugil bananensis	0 +- 0	0 +- 0	0.0	0	0
Ethmalosa dorsalis	0 +- 0	0 +- 0	0.0	0	0
Sardinella aurita	0 +- 0	0 +- 0	0.0	0	0
Sardinella maderensis	0 +- 0	0 +- 0	0.0	0	0
Dicentrarchus punctatus	0 +- 0	0 +- 0	0.0	0	0
Pomadasys spp.	0 +- 0	0 +- 0	0.0	0	0
Sarotherodon spp.	0 +- 0	0 +- 0	0.0	0	0
Smaris melanurus	0 +- 0	0 +- 0	0.0	0	0
Cheilopogon heterurus	0 +- 0	0 +- 0	0.0	0	0
Strongylura crocodila	0 +- 0	0 +- 0	0.0	0	0
Galeoides decadactylus	0 +- 0	0 +- 0	0.0	0	0
Mugil spp.	0 +- 0	0 +- 0	11.1	1	0
Liza spp.	0 +- 0	0 +- 0	0.0	0	0
Others	0 +- 0	0 +- 0	11.1	1	0
Pseudotolithus spp.	0 +- 0	0 +- 0	0.0	0	0
Caranx spp.	0 +- 0	0 +- 0	0.0	0	0
Lichia glauca	0 +- 0	0 +- 0	11.1	1	0
other Carangidae	0 +- 0	0 +- 0	0.0	0	0

Sample size = 9
Average weight = 281
Average corrected weight= 223

Mouth of the Senegal River October 1979, floodwaters
Average length and weight of fish estimated from opercula

species	length in mm	weight in g	%	number of opercula	
				all	intact
Liza dumerili	203 +- 0	97 +- 0	4.0	1	1
Liza grandisquammis	0 +- 0	0 +- 0	0.0	0	0
Liza falcipinnis	0 +- 0	0 +- 0	0.0	0	0
Mugil curema	0 +- 0	0 +- 0	0.0	0	0
Mugil monodi	0 +- 0	0 +- 0	0.0	0	0
Mugil cephalus	264 +- 29	235 +- 89	76.0	19	19
Mugil bananensis	221 +- 2	150 +- 6	8.0	2	2
Ethmalosa dorsalis	160 +- 0	77 +- 0	4.0	1	1
Sardinella aurita	0 +- 0	0 +- 0	0.0	0	0
Sardinella maderensis	0 +- 0	0 +- 0	0.0	0	0
Dicentrarchus punctatus	0 +- 0	0 +- 0	0.0	0	0
Pomadasys spp.	0 +- 0	0 +- 0	0.0	0	0
Sarotherodon spp.	0 +- 0	0 +- 0	0.0	0	0
Smaris melanurus	0 +- 0	0 +- 0	0.0	0	0
Cheilopogon heterurus	0 +- 0	0 +- 0	0.0	0	0
Strongylura crocodila	0 +- 0	0 +- 0	0.0	0	0
Galeoides decadactylus	0 +- 0	0 +- 0	0.0	0	0
Mugil spp.	0 +- 0	0 +- 0	8.0	2	0
Liza spp.	0 +- 0	0 +- 0	0.0	0	0
Others	0 +- 0	0 +- 0	0.0	0	0
Pseudotolithus spp.	0 +- 0	0 +- 0	0.0	0	0
Caranx spp.	0 +- 0	0 +- 0	0.0	0	0
Lichia glauca	0 +- 0	0 +- 0	0.0	0	0
Other Carangidae	0 +- 0	0 +- 0	0.0	0	0

Sample size = 25
Average weight = 214
Average corrected weight= 210

Mouth of the Senegal River October 1979, clear freshwater
Average length and weight of fish estimated from opercula

species	length in mm	weight in g	%	number of opercula	
				all	intact
Liza dumerili	269 +- 51	265 +-130	15.3	9	9
Liza grandisquammis	243 +- 0	168 +- 0	1.7	1	1
Liza falcipinnis	299 +- 0	299 +- 0	1.7	1	1
Mugil curema	0 +- 0	0 +- 0	0.0	0	0
Mugil monodi	0 +- 0	0 +- 0	0.0	0	0
Mugil cephalus	250 +- 27	198 +- 67	78.0	46	46
Mugil bananensis	0 +- 0	0 +- 0	0.0	0	0
Ethmalosa dorsalis	0 +- 0	0 +- 0	0.0	0	0
Sardinella aurita	0 +- 0	0 +- 0	0.0	0	0
Sardinella maderensis	0 +- 0	0 +- 0	0.0	0	0
Dicentrarchus punctatus	0 +- 0	0 +- 0	0.0	0	0
Pomadasys spp.	0 +- 0	0 +- 0	0.0	0	0
Sarotherodon spp.	276 +- 0	384 +- 0	1.7	1	1
Smaris melanurus	0 +- 0	0 +- 0	0.0	0	0
Cheilopogon heterurus	0 +- 0	0 +- 0	0.0	0	0
Strongylura crocodila	0 +- 0	0 +- 0	0.0	0	0
Galeoides decadactylus	0 +- 0	0 +- 0	0.0	0	0
Mugil spp.	0 +- 0	0 +- 0	0.0	0	0
Liza spp.	0 +- 0	0 +- 0	0.0	0	0
Others	0 +- 0	0 +- 0	1.7	1	0
Pseudotolithus spp.	0 +- 0	0 +- 0	0.0	0	0
Caranx spp.	0 +- 0	0 +- 0	0.0	0	0
Lichia glauca	0 +- 0	0 +- 0	0.0	0	0
Other Carangidae	0 +- 0	0 +- 0	0.0	0	0

Sample size = 59
Average weight = 212
Average corrected weight= 212

Mouth of the Senegal River 17 October-6 December 1979
Average length and weight of fish estimated from opercula

species	length in mm	weight in g	%	number of opercula	
				all	intact
Liza dumerili	276 +- 43	275 +-113	6.8	8	7
Liza grandisquammis	0 +- 0	0 +- 0	0.0	0	0
Liza falcipinnis	275 +- 43	243 +-132	3.4	4	4
Mugil curema	0 +- 0	0 +- 0	0.0	0	0
Mugil monodi	0 +- 0	0 +- 0	0.9	1	0
Mugil cephalus	260 +- 39	231 +-111	51.3	60	60
Mugil bananensis	264 +- 10	275 +- 38	2.6	3	3
Ethmalosa dorsalis	253 +- 9	305 +- 36	9.4	11	9
Sardinella aurita	264 +- 0	297 +- 0	0.9	1	1
Sardinella maderensis	246 +- 18	279 +- 70	12.8	15	15
Dicentrarchus punctatus	0 +- 0	0 +- 0	0.0	0	0
Pomadasys spp.	0 +- 0	0 +- 0	0.9	1	0
Sarotherodon spp.	0 +- 0	0 +- 0	0.0	0	0
Smaris melanurus	0 +- 0	0 +- 0	0.0	0	0
Cheilopogon heterurus	0 +- 0	0 +- 0	5.1	6	0
Strongylura crocodila	0 +- 0	0 +- 0	0.0	0	0
Galeoides decadactylus	0 +- 0	0 +- 0	0.0	0	0
Mugil spp.	0 +- 0	0 +- 0	5.1	6	0
Liza spp.	0 +- 0	0 +- 0	0.0	0	0
Others	0 +- 0	0 +- 0	0.9	1	0
Pseudotolithus spp.	0 +- 0	0 +- 0	0.0	0	0
Caranx spp.	0 +- 0	0 +- 0	0.0	0	0
Lichia glauca	0 +- 0	0 +- 0	0.0	0	0
Other Carangidae	0 +- 0	0 +- 0	0.0	0	0

Sample size = 117
Average weight = 247
Average corrected weight= 242

Mouth of the Senegal River 7 December 1979-28 January 1980
Average length and weight of fish estimated from opercula

species	length in mm	weight in g	%	number of opercula	
				all	intact
Liza dumerili	0 +- 0	0 +- 0	0.0	0	0
Liza grandisquammis	0 +- 0	0 +- 0	0.0	0	0
Liza falcipinnis	312 +- 31	355 +-117	5.4	11	9
Mugil curema	0 +- 0	0 +- 0	0.0	0	0
Mugil monodi	0 +- 0	0 +- 0	2.0	4	0
Mugil cephalus	282 +- 46	302 +-147	77.0	157	156
Mugil bananensis	273 +- 2	307 +- 12	1.0	2	2
Ethmalosa dorsalis	254 +- 24	317 +-103	3.9	8	5
Sardinella aurita	0 +- 0	0 +- 0	0.0	0	0
Sardinella maderensis	234 +- 28	241 +-113	2.0	4	4
Dicentrarchus punctatus	0 +- 0	0 +- 0	0.0	0	0
Pomadasys spp.	384 +- 0	878 +- 0	0.5	1	1
Sarotherodon spp.	0 +- 0	0 +- 0	0.0	0	0
Smaris melanurus	0 +- 0	0 +- 0	0.0	0	0
Cheilopogon heterurus	0 +- 0	0 +- 0	5.4	11	0
Strongylura crocodila	0 +- 0	0 +- 0	0.5	1	0
Galeoides decadactylus	0 +- 0	0 +- 0	0.5	1	0
Mugil spp.	0 +- 0	0 +- 0	2.0	4	0
Liza spp.	0 +- 0	0 +- 0	0.0	0	0
Others	0 +- 0	0 +- 0	0.0	0	0
Pseudotolithus spp.	0 +- 0	0 +- 0	0.0	0	0
Caranx spp.	0 +- 0	0 +- 0	0.0	0	0
Lichia glauca	0 +- 0	0 +- 0	0.0	0	0
Other Carangidae	0 +- 0	0 +- 0	0.0	0	0

Sample size = 204
Average weight = 301
Average corrected weight= 273

Mouth of the Senegal River February 1980
Average length and weight of fish estimated from opercula

species	length in mm	weight in g	%	number of opercula	
				all	intact
Liza dumerili	329 +- 2	452 +- 7	1.3	2	2
Liza grandisquammis	0 +- 0	0 +- 0	0.0	0	0
Liza falcipinnis	341 +- 26	468 +-127	17.9	28	28
Mugil curema	0 +- 0	0 +- 0	0.0	0	0
Mugil monodi	0 +- 0	0 +- 0	3.2	5	0
Mugil cephalus	272 +- 45	271 +-147	60.2	94	93
Mugil bananensis	207 +- 3	121 +- 7	1.3	2	2
Ethmalosa dorsalis	242 +- 13	266 +- 46	9.0	14	12
Sardinella aurita	0 +- 0	0 +- 0	0.6	1	0
Sardinella maderensis	244 +- 7	268 +- 29	2.6	4	4
Dicentrarchus punctatus	0 +- 0	0 +- 0	0.0	0	0
Pomadasys spp.	0 +- 0	0 +- 0	0.0	0	0
Sarotherodon spp.	245 +- 3	275 +- 12	2.6	4	4
Smaris melanurus	0 +- 0	0 +- 0	0.0	0	0
Cheilopogon heterurus	0 +- 0	0 +- 0	0.0	0	0
Strongylura crocodila	0 +- 0	0 +- 0	1.3	2	0
Galeoides decadactylus	0 +- 0	0 +- 0	0.0	0	0
Mugil spp.	0 +- 0	0 +- 0	0.0	0	0
Liza spp.	0 +- 0	0 +- 0	0.0	0	0
Others	0 +- 0	0 +- 0	0.0	0	0
Pseudotolithus spp.	0 +- 0	0 +- 0	0.0	0	0
Caranx spp.	0 +- 0	0 +- 0	0.0	0	0
Lichia glauca	0 +- 0	0 +- 0	0.0	0	0
Other Carangidae	0 +- 0	0 +- 0	0.0	0	0

Sample size = 156
Average weight = 296
Average corrected weight= 267

Mouth of the Senegal River March 1980
Average length and weight of fish estimated from opercula

species	length in mm	weight in g	%	number of opercula	
				all	intact
Liza dumerili	170 +- 0	56 +- 0	0.8	1	1
Liza grandisquammis	0 +- 0	0 +- 0	0.0	0	0
Liza falcipinnis	348 +- 23	496 +-102	13.2	16	16
Mugil curema	0 +- 0	0 +- 0	0.0	0	0
Mugil monodi	0 +- 0	0 +- 0	0.8	1	0
Mugil cephalus	288 +- 47	326 +-178	61.1	74	74
Mugil bananensis	215 +- 38	153 +-108	5.8	7	7
Ethmalosa dorsalis	252 +- 29	310 +-112	7.4	9	9
Sardinella aurita	263 +- 45	312 +-171	1.7	2	2
Sardinella maderensis	248 +- 2	280 +- 9	3.3	4	4
Dicentrarchus punctatus	0 +- 0	0 +- 0	0.0	0	0
Pomadasys spp.	280 +- 0	370 +- 0	1.7	2	1
Sarotherodon spp.	0 +- 0	0 +- 0	0.0	0	0
Smaris melanurus	0 +- 0	0 +- 0	0.0	0	0
Cheilopogon heterurus	0 +- 0	0 +- 0	0.0	0	0
Strongylura crocodila	0 +- 0	0 +- 0	0.0	0	0
Galeoides decadactylus	0 +- 0	0 +- 0	0.0	0	0
Mugil spp.	0 +- 0	0 +- 0	2.5	3	0
Liza spp.	0 +- 0	0 +- 0	0.0	0	0
Others	0 +- 0	0 +- 0	1.7	2	0
Pseudotolithus spp.	0 +- 0	0 +- 0	0.0	0	0
Caranx spp.	0 +- 0	0 +- 0	0.0	0	0
Lichia glauca	0 +- 0	0 +- 0	0.0	0	0
Other Carangidae	0 +- 0	0 +- 0	0.0	0	0

Sample size = 121
Average weight = 331
Average corrected weight= 286

Mouth of the Saloum River March 1979
Average length and weight of fish estimated from opercula

species	length in mm	weight in g	%	number of opercula	
				all	intact
Liza dumerili	252 +- 37	206 +- 97	11.7	9	9
Liza grandisquammis	263 +- 52	241 +-161	3.9	3	3
Liza falcipinnis	0 +- 0	0 +- 0	0.0	0	0
Mugil curema	263 +- 21	263 +- 58	6.5	5	5
Mugil monodi	0 +- 0	0 +- 0	0.0	0	0
Mugil cephalus	306 +- 55	394 +-206	11.7	9	9
Mugil bananensis	269 +- 0	291 +- 0	2.6	2	1
Ethmalosa dorsalis	263 +- 17	346 +- 72	46.7	36	25
Sardinella aurita	214 +- 24	151 +- 60	2.6	2	2
Sardinella maderensis	0 +- 0	0 +- 0	0.0	0	0
Dicentrarchus punctatus	0 +- 0	0 +- 0	0.0	0	0
Pomadasys spp.	236 +- 0	230 +- 0	2.6	2	1
Sarotherodon spp.	202 +- 0	157 +- 0	1.3	1	1
Smaris melanurus	0 +- 0	0 +- 0	0.0	0	0
Cheilopogon heterurus	0 +- 0	0 +- 0	0.0	0	0
Strongylura crocodila	0 +- 0	0 +- 0	0.0	0	0
Galeoides decadactylus	0 +- 0	0 +- 0	2.6	2	0
Mugil spp.	0 +- 0	0 +- 0	7.7	6	0
Liza spp.	0 +- 0	0 +- 0	0.0	0	0
Others	0 +- 0	0 +- 0	0.0	0	0
Pseudotolithus spp.	0 +- 0	0 +- 0	0.0	0	0
Caranx spp.	0 +- 0	0 +- 0	0.0	0	0
Lichia glauca	0 +- 0	0 +- 0	0.0	0	0
Other Carangidae	0 +- 0	0 +- 0	0.0	0	0

Sample size = 77
Average weight = 310
Average corrected weight= 294

Mouth of the Saloum River April-August 1979
Average length and weight of fish estimated from opercula

species	length in mm	weight in g	%	number of opercula	
				all	intact
Liza dumerili	260 +- 20	215 +- 49	6.5	4	3
Liza grandisquammis	282 +- 10	280 +- 35	3.2	2	2
Liza falcipinnis	277 +- 0	233 +- 0	3.2	2	1
Mugil curema	266 +- 30	282 +- 92	19.4	12	12
Mugil monodi	0 +- 0	0 +- 0	0.0	0	0
Mugil cephalus	279 +- 49	297 +-201	14.5	9	8
Mugil bananensis	252 +- 5	236 +- 19	4.8	3	3
Ethmalosa dorsalis	238 +- 29	265 +-112	43.5	27	20
Sardinella aurita	0 +- 0	0 +- 0	1.6	1	0
Sardinella maderensis	0 +- 0	0 +- 0	0.0	0	0
Dicentrarchus punctatus	0 +- 0	0 +- 0	0.0	0	0
Pomadasys spp.	0 +- 0	0 +- 0	0.0	0	0
Sarotherodon spp.	0 +- 0	0 +- 0	0.0	0	0
Smaris melanurus	0 +- 0	0 +- 0	0.0	0	0
Cheilopogon heterurus	0 +- 0	0 +- 0	0.0	0	0
Strongylura crocodila	0 +- 0	0 +- 0	0.0	0	0
Galeoides decadactylus	0 +- 0	0 +- 0	0.0	0	0
Mugil spp.	0 +- 0	0 +- 0	3.2	2	0
Liza spp.	0 +- 0	0 +- 0	0.0	0	0
Others	0 +- 0	0 +- 0	0.0	0	0
Pseudotolithus spp.	0 +- 0	0 +- 0	0.0	0	0
Caranx spp.	0 +- 0	0 +- 0	0.0	0	0
Lichia glauca	0 +- 0	0 +- 0	0.0	0	0
Other Carangidae	0 +- 0	0 +- 0	0.0	0	0

Sample size = 62
Average weight = 263
Average corrected weight= 249

Mouth of the Saloum River September-October 1979
Average length and weight of fish estimated from opercula

species	length in mm	weight in g	%	number of opercula	
				all	intact
Liza dumerili	262 +- 46	240 +-116	21.3	19	19
Liza grandisquammis	273 +- 48	265 +-152	2.2	2	2
Liza falcipinnis	266 +- 23	207 +- 59	4.5	4	4
Mugil curema	264 +- 25	279 +- 77	15.7	14	14
Mugil monodi	0 +- 0	0 +- 0	0.0	0	0
Mugil cephalus	322 +- 18	427 +- 70	10.1	9	9
Mugil bananensis	226 +- 27	171 +- 71	9.0	8	6
Ethmalosa dorsalis	264 +- 28	358 +-114	34.8	31	31
Sardinella aurita	200 +- 0	116 +- 0	1.1	1	1
Sardinella maderensis	187 +- 0	100 +- 0	1.1	1	1
Dicentrarchus punctatus	0 +- 0	0 +- 0	0.0	0	0
Pomadasys spp.	0 +- 0	0 +- 0	0.0	0	0
Sarotherodon spp.	0 +- 0	0 +- 0	0.0	0	0
Smaris melanurus	0 +- 0	0 +- 0	0.0	0	0
Cheilopogon heterurus	0 +- 0	0 +- 0	0.0	0	0
Strongylura crocodila	0 +- 0	0 +- 0	0.0	0	0
Galeoides decadactylus	0 +- 0	0 +- 0	0.0	0	0
Mugil spp.	0 +- 0	0 +- 0	0.0	0	0
Liza spp.	0 +- 0	0 +- 0	0.0	0	0
Others	0 +- 0	0 +- 0	0.0	0	0
Pseudotolithus spp.	0 +- 0	0 +- 0	0.0	0	0
Caranx spp.	0 +- 0	0 +- 0	0.0	0	0
Lichia glauca	0 +- 0	0 +- 0	0.0	0	0
Other Carangidae	0 +- 0	0 +- 0	0.0	0	0

Sample size = 89
Average weight = 296
Average corrected weight= 279

Mouth of the Saloum River November-15 December 1979
Average length and weight of fish estimated from opercula

species	length in mm	weight in g	%	number of opercula	
				all	intact
Liza dumerili	267 +- 33	244 +- 94	63.5	80	65
Liza grandisquammis	205 +- 0	93 +- 0	0.8	1	1
Liza falcipinnis	269 +- 77	244 +-201	2.4	3	2
Mugil curema	248 +- 32	234 +-101	7.1	9	8
Mugil monodi	0 +- 0	0 +- 0	0.0	0	0
Mugil cephalus	0 +- 0	0 +- 0	0.0	0	0
Mugil bananensis	243 +- 23	213 +- 64	7.1	9	9
Ethmalosa dorsalis	239 +- 26	266 +-106	11.9	15	15
Sardinella aurita	0 +- 0	0 +- 0	0.0	0	0
Sardinella maderensis	0 +- 0	0 +- 0	0.0	0	0
Dicentrarchus punctatus	192 +- 0	84 +- 0	0.8	1	1
Pomadasys spp.	250 +- 0	269 +- 0	1.6	2	1
Sarotherodon spp.	0 +- 0	0 +- 0	0.0	0	0
Smaris melanurus	0 +- 0	0 +- 0	0.0	0	0
Cheilopogon heterurus	0 +- 0	0 +- 0	0.0	0	0
Strongylura crocodila	0 +- 0	0 +- 0	0.0	0	0
Galeoides decadactylus	0 +- 0	0 +- 0	0.0	0	0
Mugil spp.	0 +- 0	0 +- 0	2.4	3	0
Liza spp.	0 +- 0	0 +- 0	0.0	0	0
Others	0 +- 0	0 +- 0	2.4	3	0
Pseudotolithus spp.	0 +- 0	0 +- 0	0.0	0	0
Caranx spp.	0 +- 0	0 +- 0	0.0	0	0
Lichia glauca	0 +- 0	0 +- 0	0.0	0	0
Other Carangidae	0 +- 0	0 +- 0	0.0	0	0

Sample size = 126
Average weight = 241
Average corrected weight= 237

Mouth of the Saloum River 15 December-15 May 1980
Average length and weight of fish estimated from opercula

species	length in mm	weight in g	%	number of opercula	
				all	intact
Liza dumerili	262 +- 35	233 +- 97	16.6	89	80
Liza grandisquammis	262 +- 31	228 +- 84	1.9	10	10
Liza falcipinnis	255 +- 34	184 +- 79	0.6	3	2
Mugil curema	248 +- 35	238 +-113	3.2	17	17
Mugil monodi	0 +- 0	0 +- 0	0.4	2	0
Mugil cephalus	303 +- 35	363 +-129	33.0	177	170
Mugil bananensis	233 +- 33	193 +- 86	4.9	26	21
Ethmalosa dorsalis	232 +- 21	239 +- 70	35.4	190	171
Sardinella aurita	298 +- 17	449 +- 80	1.3	7	7
Sardinella maderensis	0 +- 0	0 +- 0	0.0	0	0
Dicentrarchus punctatus	227 +- 0	139 +- 0	0.4	2	2
Pomadasys spp.	250 +- 29	279 +- 92	1.1	6	6
Sarotherodon spp.	170 +- 0	96 +- 0	0.2	1	1
Smaris melanurus	0 +- 0	0 +- 0	0.0	0	0
Cheilopogon heterurus	0 +- 0	0 +- 0	0.0	0	0
Strongylura crocodila	0 +- 0	0 +- 0	0.2	1	0
Galeoides decadactylus	0 +- 0	0 +- 0	0.0	0	0
Mugil spp.	0 +- 0	0 +- 0	0.0	0	0
Liza spp.	0 +- 0	0 +- 0	0.0	0	0
Others	0 +- 0	0 +- 0	0.2	1	0
Pseudotolithus spp.	0 +- 0	0 +- 0	0.8	4	0
Caranx spp.	0 +- 0	0 +- 0	0.0	0	0
Lichia glauca	0 +- 0	0 +- 0	0.0	0	0
Other Carangidae	0 +- 0	0 +- 0	0.0	0	0

Sample size = 536
Average weight = 278
Average corrected weight= 263

Djas pond north and south 2 January 1979
Average length and weight of fish estimated from opercula

species	length in mm	weight in g	%	number of opercula	
				all	intact
Liza dumerili	269 +- 35	251 +-101	10.4	61	52
Liza grandisquammis	0 +- 0	0 +- 0	0.0	0	0
Liza falcipinnis	291 +- 32	286 +- 97	39.9	233	191
Mugil curema	273 +- 30	305 +- 97	8.4	49	49
Mugil monodi	0 +- 0	0 +- 0	0.0	0	0
Mugil cephalus	265 +- 54	262 +-149	8.0	47	47
Mugil bananensis	225 +- 16	163 +- 47	9.9	58	53
Ethmalosa dorsalis	241 +- 18	267 +- 63	9.2	54	51
Sardinella aurita	245 +- 15	236 +- 48	5.0	29	28
Sardinella maderensis	223 +- 16	198 +- 51	3.3	19	19
Dicentrarchus punctatus	0 +- 0	0 +- 0	0.0	0	0
Pomadasys spp.	0 +- 0	0 +- 0	0.0	0	0
Sarotherodon spp.	230 +- 7	229 +- 21	0.3	2	2
Smaris melanurus	0 +- 0	0 +- 0	0.0	0	0
Cheilopogon heterurus	0 +- 0	0 +- 0	3.9	23	0
Strongylura crocodila	0 +- 0	0 +- 0	0.0	0	0
Galeoides decadactylus	0 +- 0	0 +- 0	0.0	0	0
Mugil spp.	0 +- 0	0 +- 0	0.7	4	0
Liza spp.	0 +- 0	0 +- 0	0.0	0	0
Others	0 +- 0	0 +- 0	0.0	0	0
Pseudotolithus spp.	0 +- 0	0 +- 0	0.0	0	0
Caranx spp.	0 +- 0	0 +- 0	0.0	0	0
Lichia glauca	0 +- 0	0 +- 0	0.0	0	0
Other Carangidae	0 +- 0	0 +- 0	0.0	0	0

Sample size = 584
Average weight = 261
Average corrected weight= 255

Djas pond north and south 2 February 1979
Average length and weight of fish estimated from opercula

species	length in mm	weight in g	%	number of opercula	
				all	intact
Liza dumerili	265 +- 34	240 +- 94	8.8	40	37
Liza grandisquammis	249 +- 0	182 +- 0	0.2	1	1
Liza falcipinnis	304 +- 36	333 +-127	27.8	126	117
Mugil curema	274 +- 25	308 +- 83	6.8	31	31
Mugil monodi	0 +- 0	0 +- 0	0.0	0	0
Mugil cephalus	273 +- 42	271 +-150	11.5	52	50
Mugil bananensis	226 +- 25	170 +- 54	6.6	30	28
Ethmalosa dorsalis	238 +- 18	258 +- 62	30.2	137	122
Sardinella aurita	258 +- 33	289 +-128	0.9	4	4
Sardinella maderensis	238 +- 18	248 +- 62	0.7	3	3
Dicentrarchus punctatus	273 +- 0	242 +- 0	0.2	1	1
Pomadasys spp.	326 +- 52	590 +-231	1.5	7	6
Sarotherodon spp.	223 +- 24	215 +- 65	2.4	11	11
Smaris melanurus	0 +- 0	0 +- 0	0.0	0	0
Cheilopogon heterurus	0 +- 0	0 +- 0	2.0	9	0
Strongylura crocodila	0 +- 0	0 +- 0	0.0	0	0
Galeoides decadactylus	0 +- 0	0 +- 0	0.0	0	0
Mugil spp.	0 +- 0	0 +- 0	0.0	0	0
Liza spp.	0 +- 0	0 +- 0	0.0	0	0
Others	0 +- 0	0 +- 0	0.0	0	0
Pseudotolithus spp.	0 +- 0	0 +- 0	0.2	1	0
Caranx spp.	0 +- 0	0 +- 0	0.0	0	0
Lichia glauca	0 +- 0	0 +- 0	0.0	0	0
Other Carangidae	0 +- 0	0 +- 0	0.2	1	0

Sample size = 454
Average weight = 280
Average corrected weight= 266

Djas pond south 14 February 1979
Average length and weight of fish estimated from opercula

species	length in mm	weight in g	%	number of opercula	
				all	intact
Liza dumerili	246 +- 20	184 +- 48	7.8	10	10
Liza grandisquammis	0 +- 0	0 +- 0	0.0	0	0
Liza falcipinnis	299 +- 40	319 +-130	30.2	39	32
Mugil curema	285 +- 24	343 +- 90	8.5	11	10
Mugil monodi	0 +- 0	0 +- 0	0.0	0	0
Mugil cephalus	307 +- 41	383 +-154	7.0	9	9
Mugil bananensis	228 +- 9	170 +- 24	12.4	16	9
Ethmalosa dorsalis	240 +- 19	265 +- 67	26.4	34	30
Sardinella aurita	0 +- 0	0 +- 0	0.0	0	0
Sardinella maderensis	250 +- 0	286 +- 0	0.8	1	1
Dicentrarchus punctatus	213 +- 0	114 +- 0	0.8	1	1
Pomadasys spp.	259 +- 13	299 +- 43	2.3	3	3
Sarotherodon spp.	219 +- 0	197 +- 0	0.8	1	1
Smaris melanurus	0 +- 0	0 +- 0	0.0	0	0
Cheilopogon heterurus	0 +- 0	0 +- 0	3.1	4	0
Strongylura crocodila	0 +- 0	0 +- 0	0.0	0	0
Galeoides decadactylus	0 +- 0	0 +- 0	0.0	0	0
Mugil spp.	0 +- 0	0 +- 0	0.0	0	0
Liza spp.	0 +- 0	0 +- 0	0.0	0	0
Others	0 +- 0	0 +- 0	0.0	0	0
Pseudotolithus spp.	0 +- 0	0 +- 0	0.0	0	0
Caranx spp.	0 +- 0	0 +- 0	0.0	0	0
Lichia glauca	0 +- 0	0 +- 0	0.0	0	0
Other Carangidae	0 +- 0	0 +- 0	0.0	0	0
	0 +- 0	0 +- 0	0.0	0	0

Sample size = 129
Average weight = 277
Average corrected weight= 264

Djas pond south 28 February 1979
Average length and weight of fish estimated from opercula

species	length in mm	weight in g	%	number of opercula	
				all	intact
Liza dumerili	274 +- 37	267 +-109	4.9	7	7
Liza grandisquammis	253 +- 4	192 +- 10	1.4	2	2
Liza falcipinnis	313 +- 36	363 +-128	32.6	47	35
Mugil curema	282 +- 24	337 +- 84	6.3	9	9
Mugil monodi	0 +- 0	0 +- 0	0.0	0	0
Mugil cephalus	308 +- 51	393 +-171	2.8	4	4
Mugil bananensis	222 +- 12	155 +- 29	9.7	14	13
Ethmalosa dorsalis	233 +- 16	240 +- 51	25.7	37	34
Sardinella aurita	282 +- 13	372 +- 53	2.1	3	3
Sardinella maderensis	229 +- 21	219 +- 69	3.5	5	5
Dicentrarchus punctatus	302 +- 22	332 +- 73	2.1	3	3
Pomadasys spp.	291 +- 41	426 +-175	4.2	6	6
Sarotherodon spp.	0 +- 0	0 +- 0	0.0	0	0
Smaris melanurus	0 +- 0	0 +- 0	0.0	0	0
Cheilopogon heterurus	0 +- 0	0 +- 0	4.2	6	0
Strongylura crocodila	0 +- 0	0 +- 0	0.0	0	0
Galeoides decadactylus	0 +- 0	0 +- 0	0.0	0	0
Mugil spp.	0 +- 0	0 +- 0	0.0	0	0
Liza spp.	0 +- 0	0 +- 0	0.0	0	0
Others	0 +- 0	0 +- 0	0.0	0	0
Pseudotolithus spp.	0 +- 0	0 +- 0	0.0	0	0
Caranx spp.	0 +- 0	0 +- 0	0.0	0	0
Lichia glauca	0 +- 0	0 +- 0	0.0	0	0
Other Carangidae	0 +- 0	0 +- 0	0.0	0	0

Sample size = 144
Average weight = 297
Average corrected weight= 279

Djas pond south 12 March 1979
Average length and weight of fish estimated from opercula

species	length in mm	weight in g	%	number of opercula	
				all	intact
Liza dumerili	259 +- 20	214 +- 49	2.3	3	3
Liza grandisquammis	272 +- 0	246 +- 0	0.8	1	1
Liza falcipinnis	310 +- 33	351 +-145	46.5	60	47
Mugil curema	285 +- 7	334 +- 41	6.2	8	8
Mugil monodi	0 +- 0	0 +- 0	0.0	0	0
Mugil cephalus	245 +- 15	180 +- 36	5.4	7	7
Mugil bananensis	236 +- 0	187 +- 0	0.8	1	1
Ethmalosa dorsalis	235 +- 25	252 +- 84	28.7	37	33
Sardinella aurita	0 +- 0	0 +- 0	0.0	0	0
Sardinella maderensis	266 +- 25	370 +-112	2.3	3	3
Dicentrarchus punctatus	287 +- 1	280 +- 2	1.6	2	2
Pomadasys spp.	265 +- 13	319 +- 43	3.1	4	4
Sarotherodon spp.	0 +- 0	0 +- 0	0.0	0	0
Smaris melanurus	0 +- 0	0 +- 0	0.0	0	0
Cheilopogon heterurus	0 +- 0	0 +- 0	1.6	2	0
Strongylura crocodila	0 +- 0	0 +- 0	0.0	0	0
Galeoides decadactylus	0 +- 0	0 +- 0	0.0	0	0
Mugil spp.	0 +- 0	0 +- 0	0.0	0	0
Liza spp.	0 +- 0	0 +- 0	0.0	0	0
Others	0 +- 0	0 +- 0	0.0	0	0
Pseudotolithus spp.	0 +- 0	0 +- 0	0.0	0	0
Caranx spp.	0 +- 0	0 +- 0	0.0	0	0
Lichia glauca	0 +- 0	0 +- 0	0.0	0	0
Other Carangidae	0 +- 0	0 +- 0	0.0	0	0

Sample size = 129
Average weight = 304
Average corrected weight= 287

Djas pond south 22-23 March 1979
Average length and weight of fish estimated from opercula

species	length in mm	weight in g	%	number of opercula	
				all	intact
Liza dumerili	257 +- 55	223 +-144	3.4	4	2
Liza grandisquammis	0 +- 0	0 +- 0	0.0	0	0
Liza falcipinnis	298 +- 34	309 +-116	49.6	58	51
Mugil curema	258 +- 24	242 +- 69	6.0	7	7
Mugil monodi	0 +- 0	0 +- 0	0.0	0	0
Mugil cephalus	231 +- 12	148 +- 26	4.3	5	5
Mugil bananensis	244 +- 28	218 +- 81	4.3	5	5
Ethmalosa dorsalis	245 +- 30	286 +-106	27.4	32	24
Sardinella aurita	0 +- 0	0 +- 0	0.0	0	0
Sardinella maderensis	242 +- 0	257 +- 0	0.9	1	1
Dicentrarchus punctatus	242 +- 22	171 +- 49	2.6	3	3
Pomadasys spp.	0 +- 0	0 +- 0	0.0	0	0
Sarotherodon spp.	195 +- 0	142 +- 0	0.9	1	1
Smaris melanurus	0 +- 0	0 +- 0	0.0	0	0
Cheilopogon heterurus	0 +- 0	0 +- 0	0.9	1	0
Strongylura crocodila	0 +- 0	0 +- 0	0.0	0	0
Galeoides decadactylus	0 +- 0	0 +- 0	0.0	0	0
Mugil spp.	0 +- 0	0 +- 0	0.0	0	0
Liza spp.	0 +- 0	0 +- 0	0.0	0	0
Others	0 +- 0	0 +- 0	0.0	0	0
Pseudotolithus spp.	0 +- 0	0 +- 0	0.0	0	0
Caranx spp.	0 +- 0	0 +- 0	0.0	0	0
Lichia glauca	0 +- 0	0 +- 0	0.0	0	0
Other Carangidae	0 +- 0	0 +- 0	0.0	0	0

Sample size = 117
Average weight = 279
Average corrected weight= 266

Djas pond south 16 April 1979
Average length and weight of fish estimated from opercula

species	length in mm	weight in g	%	number of opercula	
				all	intact
Liza dumerili	281 +- 14	274 +- 47	2.3	3	3
Liza grandisquammis	0 +- 0	0 +- 0	0.0	0	0
Liza falcipinnis	307 +- 29	336 +-105	33.1	44	32
Mugil curema	273 +- 32	301 +- 93	4.5	6	6
Mugil monodi	0 +- 0	0 +- 0	0.0	0	0
Mugil cephalus	281 +- 29	281 +- 88	3.0	4	4
Mugil bananensis	199 +- 14	107 +- 26	1.5	2	2
Ethmalosa dorsalis	236 +- 22	251 +- 73	46.6	62	53
Sardinella aurita	0 +- 0	0 +- 0	0.0	0	0
Sardinella maderensis	244 +- 46	284 +-181	1.5	2	2
Dicentrarchus punctatus	217 +- 4	121 +- 7	1.5	2	2
Pomadasys spp.	308 +- 34	493 +-147	3.8	5	5
Sarotherodon spp.	127 +- 0	42 +- 0	0.8	1	1
Smaris melanurus	0 +- 0	0 +- 0	0.0	0	0
Cheilopogon heterurus	0 +- 0	0 +- 0	0.8	1	0
Strongylura crocodila	0 +- 0	0 +- 0	0.0	0	0
Galeoides decadactylus	0 +- 0	0 +- 0	0.0	0	0
Mugil spp.	0 +- 0	0 +- 0	0.0	0	0
Liza spp.	0 +- 0	0 +- 0	0.0	0	0
Others	0 +- 0	0 +- 0	0.0	0	0
Pseudotolithus spp.	0 +- 0	0 +- 0	0.0	0	0
Caranx spp.	0 +- 0	0 +- 0	0.0	0	0
Lichia glauca	0 +- 0	0 +- 0	0.0	0	0
Other Carangidae	0 +- 0	0 +- 0	0.0	0	0

Sample size = 133
Average weight = 287
Average corrected weight= 275

Djas pond south 17-20 May 1979
Average length and weight of fish estimated from opercula

species	length in mm	weight in g	%	number of opercula	
				all	intact
Liza dumerili	255 +- 28	208 +- 83	2.3	5	5
Liza grandisquammis	0 +- 0	0 +- 0	0.0	0	0
Liza falcipinnis	349 +- 32	510 +-145	2.7	6	6
Mugil curema	238 +- 0	197 +- 0	0.9	2	2
Mugil monodi	0 +- 0	0 +- 0	0.0	0	0
Mugil cephalus	0 +- 0	0 +- 0	0.0	0	0
Mugil bananensis	0 +- 0	0 +- 0	0.0	0	0
Ethmalosa dorsalis	233 +- 21	242 +- 70	91.4	201	186
Sardinella aurita	219 +- 0	159 +- 0	0.5	1	1
Sardinella maderensis	213 +- 2	162 +- 8	0.9	2	2
Dicentrarchus punctatus	0 +- 0	0 +- 0	0.0	0	0
Pomadasys spp.	252 +- 0	276 +- 0	0.5	1	1
Sarotherodon spp.	0 +- 0	0 +- 0	0.0	0	0
Smaris melanurus	0 +- 0	0 +- 0	0.0	0	0
Cheilopogon heterurus	0 +- 0	0 +- 0	0.0	0	0
Strongylura crocodila	0 +- 0	0 +- 0	0.0	0	0
Galeoides decadactylus	0 +- 0	0 +- 0	0.0	0	0
Mugil spp.	0 +- 0	0 +- 0	0.0	0	0
Liza spp.	0 +- 0	0 +- 0	0.0	0	0
Others	0 +- 0	0 +- 0	0.0	0	0
Pseudotolithus spp.	0 +- 0	0 +- 0	0.9	2	0
Caranx spp.	0 +- 0	0 +- 0	0.0	0	0
Lichia glauca	0 +- 0	0 +- 0	0.0	0	0
Other Carangidae	0 +- 0	0 +- 0	0.0	0	0

Sample size = 220
Average weight = 247
Average corrected weight= 242

Djas pond south 6 June 1979
Average length and weight of fish estimated from opercula

species	length in mm	weight in g	%	number of opercula	
				all	intact
Liza dumerili	317 +- 0	400 +- 0	1.3	1	1
Liza grandisquammis	0 +- 0	0 +- 0	0.0	0	0
Liza falcipinnis	320 +- 39	388 +-136	5.1	4	4
Mugil curema	309 +- 1	422 +- 29	3.8	3	3
Mugil monodi	0 +- 0	0 +- 0	0.0	0	0
Mugil cephalus	0 +- 0	0 +- 0	0.0	0	0
Mugil bananensis	0 +- 0	0 +- 0	0.0	0	0
Ethmalosa dorsalis	231 +- 18	236 +- 62	86.1	68	63
Sardinella aurita	241 +- 0	221 +- 0	1.3	1	1
Sardinella maderensis	0 +- 0	0 +- 0	0.0	0	0
Dicentrarchus punctatus	326 +- 0	413 +- 0	1.3	1	1
Pomadasys spp.	246 +- 0	259 +- 0	1.3	1	1
Sarotherodon spp.	0 +- 0	0 +- 0	0.0	0	0
Smaris melanurus	0 +- 0	0 +- 0	0.0	0	0
Cheilopogon heterurus	0 +- 0	0 +- 0	0.0	0	0
Strongylura crocodila	0 +- 0	0 +- 0	0.0	0	0
Galeoides decadactylus	0 +- 0	0 +- 0	0.0	0	0
Mugil spp.	0 +- 0	0 +- 0	0.0	0	0
Liza spp.	0 +- 0	0 +- 0	0.0	0	0
Others	0 +- 0	0 +- 0	0.0	0	0
Pseudotolithus spp.	0 +- 0	0 +- 0	0.0	0	0
Caranx spp.	0 +- 0	0 +- 0	0.0	0	0
Lichia glauca	0 +- 0	0 +- 0	0.0	0	0
Other Carangidae	0 +- 0	0 +- 0	0.0	0	0

Sample size = 79
Average weight = 255
Average corrected weight= 250

Djas pond south 04-11 August 1979
Average length and weight of fish estimated from opercula

species	length in mm	weight in g	%	number of opercula	
				all	intact
Liza dumerili	0 +- 0	0 +- 0	0.0	0	0
Liza grandisquammis	0 +- 0	0 +- 0	0.0	0	0
Liza falcipinnis	0 +- 0	0 +- 0	0.0	0	0
Mugil curema	0 +- 0	0 +- 0	0.0	0	0
Mugil monodi	0 +- 0	0 +- 0	0.0	0	0
Mugil cephalus	0 +- 0	0 +- 0	0.0	0	0
Mugil bananensis	0 +- 0	0 +- 0	0.0	0	0
Ethmalosa dorsalis	245 +- 21	280 +- 80	90.0	9	9
Sardinella aurita	299 +- 0	448 +- 0	10.0	1	1
Sardinella maderensis	0 +- 0	0 +- 0	0.0	0	0
Dicentrarchus punctatus	0 +- 0	0 +- 0	0.0	0	0
Pomadasys spp.	0 +- 0	0 +- 0	0.0	0	0
Sarotherodon spp.	0 +- 0	0 +- 0	0.0	0	0
Smaris melanurus	0 +- 0	0 +- 0	0.0	0	0
Cheilopogon heterurus	0 +- 0	0 +- 0	0.0	0	0
Strongylura crocodila	0 +- 0	0 +- 0	0.0	0	0
Galeoides decadactylus	0 +- 0	0 +- 0	0.0	0	0
Mugil spp.	0 +- 0	0 +- 0	0.0	0	0
Liza spp.	0 +- 0	0 +- 0	0.0	0	0
Others	0 +- 0	0 +- 0	0.0	0	0
Pseudotolithus spp.	0 +- 0	0 +- 0	0.0	0	0
Caranx spp.	0 +- 0	0 +- 0	0.0	0	0
Lichia glauca	0 +- 0	0 +- 0	0.0	0	0
Other Carangidae	0 +- 0	0 +- 0	0.0	0	0

Sample size = 10
Average weight = 296
Average corrected weight= 286

Djas pond south 28-30 August 1979
Average length and weight of fish estimated from opercula

species	length in mm	weight in g	%	number of opercula	
				all	intact
Liza dumerili	0 +- 0	0 +- 0	0.0	0	0
Liza grandisquammis	0 +- 0	0 +- 0	0.0	0	0
Liza falcipinnis	0 +- 0	0 +- 0	0.0	0	0
Mugil curema	0 +- 0	0 +- 0	0.0	0	0
Mugil monodi	0 +- 0	0 +- 0	0.0	0	0
Mugil cephalus	276 +- 14	261 +- 44	64.7	11	11
Mugil bananensis	0 +- 0	0 +- 0	0.0	0	0
Ethmalosa dorsalis	226 +- 5	216 +- 15	29.4	5	5
Sardinella aurita	0 +- 0	0 +- 0	0.0	0	0
Sardinella maderensis	0 +- 0	0 +- 0	0.0	0	0
Dicentrarchus punctatus	0 +- 0	0 +- 0	0.0	0	0
Pomadasys spp.	0 +- 0	0 +- 0	0.0	0	0
Sarotherodon spp.	216 +- 0	191 +- 0	5.9	1	1
Smaris melanurus	0 +- 0	0 +- 0	0.0	0	0
Cheilopogon heterurus	0 +- 0	0 +- 0	0.0	0	0
Strongylura crocodila	0 +- 0	0 +- 0	0.0	0	0
Galeoides decadactylus	0 +- 0	0 +- 0	0.0	0	0
Mugil spp.	0 +- 0	0 +- 0	0.0	0	0
Liza spp.	0 +- 0	0 +- 0	0.0	0	0
Others	0 +- 0	0 +- 0	0.0	0	0
Pseudotolithus spp.	0 +- 0	0 +- 0	0.0	0	0
Caranx spp.	0 +- 0	0 +- 0	0.0	0	0
Lichia glauca	0 +- 0	0 +- 0	0.0	0	0
Other Carangidae	0 +- 0	0 +- 0	0.0	0	0

Sample size = 17
Average weight = 243
Average corrected weight= 243

Djas pond south 23-30 October 1979
Average length and weight of fish estimated from opercula

species	length in mm	weight in g	%	number of opercula	
				all	intact
Liza dumerili	266 +- 19	234 +- 50	5.3	5	5
Liza grandisquammis	0 +- 0	0 +- 0	0.0	0	0
Liza falcipinnis	274 +- 37	238 +-102	5.3	5	5
Mugil curema	297 +- 23	362 +- 52	2.1	2	2
Mugil monodi	0 +- 0	0 +- 0	0.0	0	0
Mugil cephalus	286 +- 32	301 +- 95	72.6	69	67
Mugil bananensis	200 +- 0	107 +- 0	1.1	1	1
Ethmalosa dorsalis	226 +- 9	216 +- 24	8.4	8	7
Sardinella aurita	0 +- 0	0 +- 0	0.0	0	0
Sardinella maderensis	291 +- 0	494 +- 0	1.1	1	1
Dicentrarchus punctatus	272 +- 0	237 +- 0	1.1	1	1
Pomadasys spp.	227 +- 0	207 +- 1	2.1	2	2
Sarotherodon spp.	0 +- 0	0 +- 0	0.0	0	0
Smaris melanurus	0 +- 0	0 +- 0	0.0	0	0
Cheilopogon heterurus	0 +- 0	0 +- 0	0.0	0	0
Strongylura crocodila	0 +- 0	0 +- 0	0.0	0	0
Galeoides decadactylus	0 +- 0	0 +- 0	0.0	0	0
Mugil spp.	0 +- 0	0 +- 0	0.0	0	0
Liza spp.	0 +- 0	0 +- 0	0.0	0	0
Others	0 +- 0	0 +- 0	0.0	0	0
Pseudotolithus spp.	0 +- 0	0 +- 0	0.0	0	0
Caranx spp.	0 +- 0	0 +- 0	0.0	0	0
Lichia glauca	0 +- 0	0 +- 0	0.0	0	0
Other Carangidae	0 +- 0	0 +- 0	0.0	0	0

Sample size = 95
Average weight = 285
Average corrected weight= 278

Djas pond south 15 November 1979
Average length and weight of fish estimated from opercula

species	length in mm	weight in g	%	number of opercula	
				all	intact
Liza dumerili	237 +- 3	159 +- 7	6.9	2	2
Liza grandisquammis	0 +- 0	0 +- 0	0.0	0	0
Liza falcipinnis	265 +- 2	202 +- 6	10.3	3	3
Mugil curema	0 +- 0	0 +- 0	0.0	0	0
Mugil monodi	0 +- 0	0 +- 0	0.0	0	0
Mugil cephalus	318 +- 24	413 +- 90	55.2	16	16
Mugil bananensis	234 +- 9	182 +- 24	6.9	2	2
Ethmalosa dorsalis	252 +- 12	301 +- 45	17.2	5	4
Sardinella aurita	0 +- 0	0 +- 0	0.0	0	0
Sardinella maderensis	0 +- 0	0 +- 0	0.0	0	0
Dicentrarchus punctatus	290 +- 0	291 +- 0	3.4	1	1
Pomadasys spp.	0 +- 0	0 +- 0	0.0	0	0
Sarotherodon spp.	0 +- 0	0 +- 0	0.0	0	0
Smaris melanurus	0 +- 0	0 +- 0	0.0	0	0
Cheilopogon heterurus	0 +- 0	0 +- 0	0.0	0	0
Strongylura crocodila	0 +- 0	0 +- 0	0.0	0	0
Galeoides decadactylus	0 +- 0	0 +- 0	0.0	0	0
Mugil spp.	0 +- 0	0 +- 0	0.0	0	0
Liza spp.	0 +- 0	0 +- 0	0.0	0	0
Others	0 +- 0	0 +- 0	0.0	0	0
Pseudotolithus spp.	0 +- 0	0 +- 0	0.0	0	0
Caranx spp.	0 +- 0	0 +- 0	0.0	0	0
Lichia glauca	0 +- 0	0 +- 0	0.0	0	0
Other Carangidae	0 +- 0	0 +- 0	0.0	0	0

Sample size = 29
Average weight = 334
Average corrected weight= 309

Djas pond south 11-23 December 1979
Average length and weight of fish estimated from opercula

species	length in mm	weight in g	%	number of opercula	
				all	intact
Liza dumerili	269 +- 42	256 +-118	8.0	9	8
Liza grandisquammis	0 +- 0	0 +- 0	0.0	0	0
Liza falcipinnis	286 +- 33	270 +-112	8.0	9	9
Mugil curema	264 +- 41	289 +-136	6.2	7	5
Mugil monodi	0 +- 0	0 +- 0	0.0	0	0
Mugil cephalus	311 +- 39	397 +-126	18.7	21	21
Mugil bananensis	207 +- 22	123 +- 44	1.8	2	2
Ethmalosa dorsalis	246 +- 13	283 +- 47	47.3	53	50
Sardinella aurita	301 +- 2	459 +- 11	2.7	3	3
Sardinella maderensis	232 +- 0	220 +- 0	1.8	2	2
Dicentrarchus punctatus	345 +- 36	504 +-164	1.8	2	2
Pomadasys spp.	318 +- 7	522 +- 32	1.8	2	2
Sarotherodon spp.	264 +- 2	338 +- 12	1.8	2	2
Smaris melanurus	0 +- 0	0 +- 0	0.0	0	0
Cheilopogon heterurus	0 +- 0	0 +- 0	0.9	1	0
Strongylura crocodila	0 +- 0	0 +- 0	0.0	0	0
Galeoides decadactylus	0 +- 0	0 +- 0	0.0	0	0
Mugil spp.	0 +- 0	0 +- 0	0.0	0	0
Liza spp.	0 +- 0	0 +- 0	0.0	0	0
Others	0 +- 0	0 +- 0	0.0	0	0
Pseudotolithus spp.	0 +- 0	0 +- 0	0.0	0	0
Caranx spp.	0 +- 0	0 +- 0	0.0	0	0
Lichia glauca	0 +- 0	0 +- 0	0.0	0	0
Other Carangidae	0 +- 0	0 +- 0	0.0	0	0

Sample size = 113
Average weight = 311
Average corrected weight= 295

Djas pond north 14 February 1979
Average length and weight of fish estimated from opercula

species	length in mm	weight in g	%	number of opercula	
				all	intact
Liza dumerili	254 +- 19	201 +- 50	6.3	7	6
Liza grandisquammis	0 +- 0	0 +- 0	0.0	0	0
Liza falcipinnis	304 +- 38	333 +-138	56.3	63	61
Mugil curema	272 +- 70	345 +-240	3.6	4	4
Mugil monodi	0 +- 0	0 +- 0	0.0	0	0
Mugil cephalus	255 +- 26	210 +- 71	14.3	16	16
Mugil bananensis	236 +- 11	189 +- 28	7.1	8	7
Ethmalosa dorsalis	243 +- 25	278 +- 85	8.9	10	10
Sardinella aurita	0 +- 0	0 +- 0	0.0	0	0
Sardinella maderensis	0 +- 0	0 +- 0	0.0	0	0
Dicentrarchus punctatus	301 +- 0	324 +- 0	0.9	1	1
Pomadasys spp.	214 +- 0	175 +- 0	0.9	1	1
Sarotherodon spp.	0 +- 0	0 +- 0	0.0	0	0
Smaris melanurus	0 +- 0	0 +- 0	0.0	0	0
Cheilopogon heterurus	0 +- 0	0 +- 0	0.9	1	0
Strongylura crocodila	0 +- 0	0 +- 0	0.0	0	0
Galeoides decadactylus	0 +- 0	0 +- 0	0.0	0	0
Mugil spp.	0 +- 0	0 +- 0	0.0	0	0
Liza spp.	0 +- 0	0 +- 0	0.0	0	0
Others	0 +- 0	0 +- 0	0.0	0	0
Pseudotolithus spp.	0 +- 0	0 +- 0	0.0	0	0
Caranx spp.	0 +- 0	0 +- 0	0.0	0	0
Lichia glauca	0 +- 0	0 +- 0	0.0	0	0
Other Carangidae	0 +- 0	0 +- 0	0.0	0	0

Sample size = 112
Average weight = 290
Average corrected weight= 268

Djas pond north 28 February 1979
Average length and weight of fish estimated from opercula

species	length in mm	weight in g	%	number of opercula	
				all	intact
Liza dumerili	256 +- 35	214 +- 83	9.8	5	5
Liza grandisquammis	0 +- 0	0 +- 0	0.0	0	0
Liza falcipinnis	333 +- 32	438 +-145	56.9	29	22
Mugil curema	286 +- 2	322 +- 26	3.9	2	2
Mugil monodi	0 +- 0	0 +- 0	0.0	0	0
Mugil cephalus	279 +- 50	282 +-154	3.9	2	2
Mugil bananensis	239 +- 0	195 +- 0	2.0	1	1
Ethmalosa dorsalis	242 +- 19	268 +- 64	23.5	12	10
Sardinella aurita	0 +- 0	0 +- 0	0.0	0	0
Sardinella maderensis	0 +- 0	0 +- 0	0.0	0	0
Dicentrarchus punctatus	0 +- 0	0 +- 0	0.0	0	0
Pomadasys spp.	0 +- 0	0 +- 0	0.0	0	0
Sarotherodon spp.	0 +- 0	0 +- 0	0.0	0	0
Smaris melanurus	0 +- 0	0 +- 0	0.0	0	0
Cheilopogon heterurus	0 +- 0	0 +- 0	0.0	0	0
Strongylura crocodila	0 +- 0	0 +- 0	0.0	0	0
Galeoides decadactylus	0 +- 0	0 +- 0	0.0	0	0
Mugil spp.	0 +- 0	0 +- 0	0.0	0	0
Liza spp.	0 +- 0	0 +- 0	0.0	0	0
Others	0 +- 0	0 +- 0	0.0	0	0
Pseudotolithus spp.	0 +- 0	0 +- 0	0.0	0	0
Caranx spp.	0 +- 0	0 +- 0	0.0	0	0
Lichia glauca	0 +- 0	0 +- 0	0.0	0	0
Other Carangidae	0 +- 0	0 +- 0	0.0	0	0

Sample size = 51
Average weight = 360
Average corrected weight= 320

Djas pond north 9 March 1979
Average length and weight of fish estimated from opercula

species	length in mm	weight in g	%	number of opercula	
				all	intact
Liza dumerili	0 +- 0	0 +- 0	0.0	0	0
Liza grandisquammis	0 +- 0	0 +- 0	0.0	0	0
Liza falcipinnis	322 +- 29	394 +-121	56.4	31	25
Mugil curema	268 +- 17	282 +- 69	10.9	6	6
Mugil monodi	0 +- 0	0 +- 0	0.0	0	0
Mugil cephalus	275 +- 49	277 +-163	5.5	3	3
Mugil bananensis	228 +- 23	172 +- 57	7.3	4	4
Ethmalosa dorsalis	238 +- 15	255 +- 47	12.7	7	5
Sardinella aurita	0 +- 0	0 +- 0	0.0	0	0
Sardinella maderensis	214 +- 0	165 +- 0	1.8	1	1
Dicentrarchus punctatus	275 +- 0	245 +- 0	1.8	1	1
Pomadasys spp.	239 +- 0	237 +- 0	1.8	1	1
Sarotherodon spp.	0 +- 0	0 +- 0	0.0	0	0
Smaris melanurus	0 +- 0	0 +- 0	0.0	0	0
Cheilopogon heterurus	0 +- 0	0 +- 0	0.0	0	0
Strongylura crocodila	0 +- 0	0 +- 0	0.0	0	0
Galeoides decadactylus	0 +- 0	0 +- 0	0.0	0	0
Mugil spp.	0 +- 0	0 +- 0	0.0	0	0
Liza spp.	0 +- 0	0 +- 0	0.0	0	0
Others	0 +- 0	0 +- 0	0.0	0	0
Pseudotolithus spp.	0 +- 0	0 +- 0	0.0	0	0
Caranx spp.	0 +- 0	0 +- 0	0.0	0	0
Lichia glauca	0 +- 0	0 +- 0	0.0	0	0
Other Carangidae	0 +- 0	0 +- 0	0.0	0	0

Sample size = 55
Average weight = 330
Average corrected weight= 303

Djas pond north 21-23 March 1979
Average length and weight of fish estimated from opercula

species	length in mm	weight in g	%	number of opercula	
				all	intact
Liza dumerili	272 +- 21	250 +- 62	10.5	13	13
Liza grandisquammis	0 +- 0	0 +- 0	0.0	0	0
Liza falcipinnis	315 +- 29	364 +-113	56.5	70	49
Mugil curema	264 +- 30	280 +- 94	4.0	5	5
Mugil monodi	0 +- 0	0 +- 0	0.0	0	0
Mugil cephalus	261 +- 27	225 +- 80	4.8	6	6
Mugil bananensis	243 +- 0	208 +- 1	3.2	4	3
Ethmalosa dorsalis	247 +- 21	288 +- 74	15.3	19	16
Sardinella aurita	0 +- 0	0 +- 0	0.0	0	0
Sardinella maderensis	266 +- 1	360 +- 7	1.6	2	2
Dicentrarchus punctatus	0 +- 0	0 +- 0	0.0	0	0
Pomadasys spp.	276 +- 3	356 +- 10	1.6	2	2
Sarotherodon spp.	0 +- 0	0 +- 0	0.0	0	0
Smaris melanurus	0 +- 0	0 +- 0	0.0	0	0
Cheilopogon heterurus	0 +- 0	0 +- 0	0.0	0	0
Strongylura crocodila	0 +- 0	0 +- 0	0.0	0	0
Galeoides decadactylus	0 +- 0	0 +- 0	0.0	0	0
Mugil spp.	0 +- 0	0 +- 0	0.0	0	0
Liza spp.	0 +- 0	0 +- 0	0.0	0	0
Others	0 +- 0	0 +- 0	2.4	3	0
Pseudotolithus spp.	0 +- 0	0 +- 0	0.0	0	0
Caranx spp.	0 +- 0	0 +- 0	0.0	0	0
Lichia glauca	0 +- 0	0 +- 0	0.0	0	0
Other Carangidae	0 +- 0	0 +- 0	0.0	0	0

Sample size = 124
Average weight = 324
Average corrected weight= 305

Djas pond north 14 April 1979
Average length and weight of fish estimated from opercula

species	length in mm	weight in g	%	number of opercula	
				all	intact
Liza dumerili	234 +- 0	152 +- 0	2.6	1	1
Liza grandisquammis	0 +- 0	0 +- 0	0.0	0	0
Liza falcipinnis	310 +- 30	348 +-118	30.8	12	9
Mugil curema	255 +- 14	244 +- 41	5.1	2	2
Mugil monodi	0 +- 0	0 +- 0	0.0	0	0
Mugil cephalus	250 +- 21	191 +- 49	5.1	2	2
Mugil bananensis	228 +- 3	168 +- 7	7.7	3	3
Ethmalosa dorsalis	254 +- 23	314 +- 85	46.2	18	13
Sardinella aurita	0 +- 0	0 +- 0	0.0	0	0
Sardinella maderensis	0 +- 0	0 +- 0	0.0	0	0
Dicentrarchus punctatus	0 +- 0	0 +- 0	0.0	0	0
Pomadasys spp.	349 +- 0	676 +- 0	2.6	1	1
Sarotherodon spp.	0 +- 0	0 +- 0	0.0	0	0
Smaris melanurus	0 +- 0	0 +- 0	0.0	0	0
Cheilopogon heterurus	0 +- 0	0 +- 0	0.0	0	0
Strongylura crocodila	0 +- 0	0 +- 0	0.0	0	0
Galeoides decadactylus	0 +- 0	0 +- 0	0.0	0	0
Mugil spp.	0 +- 0	0 +- 0	0.0	0	0
Liza spp.	0 +- 0	0 +- 0	0.0	0	0
Others	0 +- 0	0 +- 0	0.0	0	0
Pseudotolithus spp.	0 +- 0	0 +- 0	0.0	0	0
Caranx spp.	0 +- 0	0 +- 0	0.0	0	0
Lichia glauca	0 +- 0	0 +- 0	0.0	0	0
Other Carangidae	0 +- 0	0 +- 0	0.0	0	0

Sample size = 39
Average weight = 308
Average corrected weight= 288

Djas pond north 15 May 1979
Average length and weight of fish estimated from opercula

species	length in mm	weight in g	%	number of opercula	
				all	intact
Liza dumerili	281 +- 26	282 +- 85	13.6	16	14
Liza grandisquammis	0 +- 0	0 +- 0	0.0	0	0
Liza falcipinnis	300 +- 31	312 +-113	21.4	25	22
Mugil curema	261 +- 65	304 +-229	4.3	5	5
Mugil monodi	0 +- 0	0 +- 0	1.7	2	0
Mugil cephalus	249 +- 70	237 +-206	8.5	10	10
Mugil bananensis	220 +- 3	149 +- 8	4.3	5	5
Ethmalosa dorsalis	241 +- 19	268 +- 61	29.1	34	33
Sardinella aurita	282 +- 2	372 +- 11	1.7	2	2
Sardinella maderensis	237 +- 11	242 +- 41	4.3	5	5
Dicentrarchus punctatus	279 +- 34	270 +-108	5.1	6	6
Pomadasys spp.	286 +- 0	393 +- 2	1.7	2	2
Sarotherodon spp.	0 +- 0	0 +- 0	0.0	0	0
Smaris melanurus	0 +- 0	0 +- 0	0.0	0	0
Cheilopogon heterurus	0 +- 0	0 +- 0	0.9	1	0
Strongylura crocodila	0 +- 0	0 +- 0	0.0	0	0
Galeoides decadactylus	0 +- 0	0 +- 0	0.9	1	0
Mugil spp.	0 +- 0	0 +- 0	0.0	0	0
Liza spp.	0 +- 0	0 +- 0	0.0	0	0
Others	0 +- 0	0 +- 0	0.0	0	0
Pseudotolithus spp.	0 +- 0	0 +- 0	0.0	0	0
Caranx spp.	0 +- 0	0 +- 0	0.0	0	0
Lichia glauca	0 +- 0	0 +- 0	0.0	0	0
Other Carangidae	0 +- 0	0 +- 0	0.0	0	0

Sample size = 117
Average weight = 271
Average corrected weight= 261

Djas pond north 29 August 1979
Average length and weight of fish estimated from opercula

species	length in mm	weight in g	%	number of opercula	
				all	intact
Liza dumerili	0 +- 0	0 +- 0	0.0	0	0
Liza grandisquammis	0 +- 0	0 +- 0	0.0	0	0
Liza falcipinnis	0 +- 0	0 +- 0	0.0	0	0
Mugil curema	0 +- 0	0 +- 0	0.0	0	0
Mugil monodi	0 +- 0	0 +- 0	0.0	0	0
Mugil cephalus	293 +- 8	315 +- 27	50.0	4	4
Mugil bananensis	0 +- 0	0 +- 0	0.0	0	0
Ethmalosa dorsalis	217 +- 25	196 +- 70	50.0	4	4
Sardinella aurita	0 +- 0	0 +- 0	0.0	0	0
Sardinella maderensis	0 +- 0	0 +- 0	0.0	0	0
Dicentrarchus punctatus	0 +- 0	0 +- 0	0.0	0	0
Pomadasys spp.	0 +- 0	0 +- 0	0.0	0	0
Sarotherodon spp.	0 +- 0	0 +- 0	0.0	0	0
Smaris melanurus	0 +- 0	0 +- 0	0.0	0	0
Cheilopogon heterurus	0 +- 0	0 +- 0	0.0	0	0
Strongylura crocodila	0 +- 0	0 +- 0	0.0	0	0
Galeoides decadactylus	0 +- 0	0 +- 0	0.0	0	0
Mugil spp.	0 +- 0	0 +- 0	0.0	0	0
Liza spp.	0 +- 0	0 +- 0	0.0	0	0
Others	0 +- 0	0 +- 0	0.0	0	0
Pseudotolithus spp.	0 +- 0	0 +- 0	0.0	0	0
Caranx spp.	0 +- 0	0 +- 0	0.0	0	0
Lichia glauca	0 +- 0	0 +- 0	0.0	0	0
Other Carangidae	0 +- 0	0 +- 0	0.0	0	0

Sample size = 8
Average weight = 255
Average corrected weight= 255

Djas pond north 25-30 October 1979
Average length and weight of fish estimated from opercula

species	length in mm	weight in g	%	number of opercula	
				all	intact
Liza dumerili	239 +- 20	167 +- 46	6.3	4	4
Liza grandisquammis	0 +- 0	0 +- 0	0.0	0	0
Liza falcipinnis	323 +- 10	387 +- 43	7.9	5	5
Mugil curema	263 +- 2	267 +- 7	4.8	3	2
Mugil monodi	0 +- 0	0 +- 0	0.0	0	0
Mugil cephalus	278 +- 44	287 +-125	68.3	43	41
Mugil bananensis	222 +- 20	156 +- 47	9.5	6	4
Ethmalosa dorsalis	249 +- 4	290 +- 15	3.2	2	2
Sardinella aurita	0 +- 0	0 +- 0	0.0	0	0
Sardinella maderensis	0 +- 0	0 +- 0	0.0	0	0
Dicentrarchus punctatus	0 +- 0	0 +- 0	0.0	0	0
Pomadasys spp.	0 +- 0	0 +- 0	0.0	0	0
Sarotherodon spp.	0 +- 0	0 +- 0	0.0	0	0
Smaris melanurus	0 +- 0	0 +- 0	0.0	0	0
Cheilopogon heterurus	0 +- 0	0 +- 0	0.0	0	0
Strongylura crocodila	0 +- 0	0 +- 0	0.0	0	0
Galeoides decadactylus	0 +- 0	0 +- 0	0.0	0	0
Mugil spp.	0 +- 0	0 +- 0	0.0	0	0
Liza spp.	0 +- 0	0 +- 0	0.0	0	0
Others	0 +- 0	0 +- 0	0.0	0	0
Pseudotolithus spp.	0 +- 0	0 +- 0	0.0	0	0
Caranx spp.	0 +- 0	0 +- 0	0.0	0	0
Lichia glauca	0 +- 0	0 +- 0	0.0	0	0
Other Carangidae	0 +- 0	0 +- 0	0.0	0	0

Sample size = 63
Average weight = 273
Average corrected weight= 264

Djas pond north 15 November 1979
Average length and weight of fish estimated from opercula

species	length in mm	weight in g	%	number of opercula	
				all	intact
Liza dumerili	235 +- 25	159 +- 52	10.9	6	4
Liza grandisquammis	0 +- 0	0 +- 0	0.0	0	0
Liza falcipinnis	262 +- 81	251 +-226	9.1	5	5
Mugil curema	238 +- 19	197 +- 43	12.7	7	7
Mugil monodi	0 +- 0	0 +- 0	0.0	0	0
Mugil cephalus	217 +- 35	132 +- 74	49.1	27	27
Mugil bananensis	220 +- 17	152 +- 41	12.7	7	7
Ethmalosa dorsalis	0 +- 0	0 +- 0	0.0	0	0
Sardinella aurita	0 +- 0	0 +- 0	0.0	0	0
Sardinella maderensis	0 +- 0	0 +- 0	0.0	0	0
Dicentrarchus punctatus	330 +- 0	429 +- 0	1.8	1	1
Pomadasys spp.	0 +- 0	0 +- 0	0.0	0	0
Sarotherodon spp.	176 +- 2	107 +- 4	3.6	2	2
Smaris melanurus	0 +- 0	0 +- 0	0.0	0	0
Cheilopogon heterurus	0 +- 0	0 +- 0	0.0	0	0
Strongylura crocodila	0 +- 0	0 +- 0	0.0	0	0
Galeoides decadactylus	0 +- 0	0 +- 0	0.0	0	0
Mugil spp.	0 +- 0	0 +- 0	0.0	0	0
Liza spp.	0 +- 0	0 +- 0	0.0	0	0
Others	0 +- 0	0 +- 0	0.0	0	0
Pseudotolithus spp.	0 +- 0	0 +- 0	0.0	0	0
Caranx spp.	0 +- 0	0 +- 0	0.0	0	0
Lichia glauca	0 +- 0	0 +- 0	0.0	0	0
Other Carangidae	0 +- 0	0 +- 0	0.0	0	0

Sample size = 55
Average weight = 161
Average corrected weight= 157

Djas pond north 13-21 December 1979
Average length and weight of fish estimated from opercula

species	length in mm	weight in g	%	number of opercula	
				all	intact
Liza dumerili	262 +- 35	232 +- 96	25.7	47	44
Liza grandisquammis	0 +- 0	0 +- 0	0.0	0	0
Liza falcipinnis	260 +- 35	202 +- 82	14.2	26	24
Mugil curema	238 +- 47	212 +-119	3.8	7	7
Mugil monodi	0 +- 0	0 +- 0	0.5	1	0
Mugil cephalus	227 +- 50	166 +-137	21.9	40	40
Mugil bananensis	209 +- 14	128 +- 31	10.9	20	19
Ethmalosa dorsalis	243 +- 11	271 +- 38	20.2	37	36
Sardinella aurita	282 +- 3	373 +- 16	1.6	3	3
Sardinella maderensis	0 +- 0	0 +- 0	0.0	0	0
Dicentrarchus punctatus	276 +- 91	295 +-258	1.1	2	2
Pomadasys spp.	0 +- 0	0 +- 0	0.0	0	0
Sarotherodon spp.	0 +- 0	0 +- 0	0.0	0	0
Smaris melanurus	0 +- 0	0 +- 0	0.0	0	0
Cheilopogon heterurus	0 +- 0	0 +- 0	0.0	0	0
Strongylura crocodila	0 +- 0	0 +- 0	0.0	0	0
Galeoides decadactylus	0 +- 0	0 +- 0	0.0	0	0
Mugil spp.	0 +- 0	0 +- 0	0.0	0	0
Liza spp.	0 +- 0	0 +- 0	0.0	0	0
Others	0 +- 0	0 +- 0	0.0	0	0
Pseudotolithus spp.	0 +- 0	0 +- 0	0.0	0	0
Caranx spp.	0 +- 0	0 +- 0	0.0	0	0
Lichia glauca	0 +- 0	0 +- 0	0.0	0	0
Other Carangidae	0 +- 0	0 +- 0	0.0	0	0

Sample size = 183
Average weight = 210
Average corrected weight= 207

Djas pond north 20 May 1980
Average length and weight of fish estimated from opercula

species	length in mm	weight in g	%	number of opercula	
				all	intact
Liza dumerili	201 +- 27	282 +- 86	13.7	16	14
Liza grandisquammis	0 +- 0	0 +- 0	0.0	0	0
Liza falcipinnis	300 +- 31	313 +-113	21.4	25	22
Mugil curema	261 +- 65	305 +-230	4.3	5	5
Mugil monodi	0 +- 0	0 +- 0	1.7	2	0
Mugil cephalus	249 +- 70	237 +-207	8.5	10	10
Mugil bananensis	220 +- 3	149 +- 9	4.3	5	5
Ethmalosa dorsalis	411 +-20	266 +- 63	29.1	34	33
Sardinella aurita	282 +- 2	372 +- 11	1.7	2	2
Sardinella maderensis	237 +- 12	243 +- 42	4.3	5	5
Dicentrarchus punctatus	279 +- 35	271 +-109	5.1	6	6
Pomadasys spp.	286 +- 1	393 +- 0	1.7	2	2
Sarotherodon spp.	0 +- 0	0 +- 0	0.0	0	0
Smaris melanurus	0 +- 0	0 +- 0	0.0	0	0
Cheilopogon heterurus	0 +- 0	0 +- 0	0.0	1	0
Strongylura crocodila	0 +- 0	0 +- 0	0.0	0	0
Galeoides decadactylus	0 +- 0	0 +- 0	0.0	1	0
Mugil spp.	0 +- 0	0 +- 0	0.0	0	0
Liza spp.	0 +- 0	0 +- 0	0.0	0	0
Others	0 +- 0	0 +- 0	0.0	3	0
Pseudotolithus spp.	0 +- 0	0 +- 0	0.0	0	0
Caranx spp.	0 +- 0	0 +- 0	0.0	0	0
Lichia glauca	0 +- 0	0 +- 0	0.0	0	0
Other Carangidae	0 +- 0	0 +- 0	0.0	0	0

Sample size = 117
Average weight = 271
Average corrected weight= 261

Ile aux Oiseaux February 1979
Average length and weight of fish estimated from opercula

species	length in mm	weight in g	%	number of opercula	
				all	intact
Liza dumerili	379 +- 0	709 +- 0	2.3	1	1
Liza grandisquammis	254 +- 37	210 +-108	11.6	5	5
Liza falcipinnis	0 +- 0	0 +- 0	0.0	0	0
Mugil curema	211 +- 45	147 +- 91	4.7	2	2
Mugil monodi	0 +- 0	0 +- 0	0.0	0	0
Mugil cephalus	0 +- 0	0 +- 0	0.0	0	0
Mugil bananensis	217 +- 26	150 +- 56	69.8	30	18
Ethmalosa dorsalis	227 +- 34	226 +- 99	4.7	2	2
Sardinella aurita	0 +- 0	0 +- 0	0.0	0	0
Sardinella maderensis	0 +- 0	0 +- 0	0.0	0	0
Dicentrarchus punctatus	0 +- 0	0 +- 0	0.0	0	0
Pomadasys spp.	0 +- 0	0 +- 0	0.0	0	0
Sarotherodon spp.	239 +- 18	256 +- 53	7.0	3	3
Smaris melanurus	0 +- 0	0 +- 0	0.0	0	0
Cheilopogon heterurus	0 +- 0	0 +- 0	0.0	0	0
Strongylura crocodila	0 +- 0	0 +- 0	0.0	0	0
galeoides decadactylus	0 +- 0	0 +- 0	0.0	0	0
Mugil spp.	0 +- 0	0 +- 0	0.0	0	0
Liza spp.	0 +- 0	0 +- 0	0.0	0	0
Others	0 +- 0	0 +- 0	0.0	0	0
Pseudotolithus spp.	0 +- 0	0 +- 0	0.0	0	0
Caranx spp.	0 +- 0	0 +- 0	0.0	0	0
Lichia glauca	0 +- 0	0 +- 0	0.0	0	0
Other Carangidae	0 +- 0	0 +- 0	0.0	0	0

Sample size = 43
Average weight = 180
Average corrected weight= 173

Ile aux Oiseaux Mars 1979
Average length and weight of fish estimated from opercula

species	length in mm	weight in g	%	number of opercula	
				all	intact
Liza dumerili	225 +- 50	151 +-111	4.2	3	3
Liza grandisquammis	255 +- 35	212 +- 94	25.0	18	18
Liza falcipinnis	0 +- 0	0 +- 0	0.0	0	0
Mugil curema	254 +- 30	240 +- 81	15.3	11	10
Mugil monodi	0 +- 0	0 +- 0	0.0	0	0
Mugil cephalus	0 +- 0	0 +- 0	0.0	0	0
Mugil bananensis	219 +- 20	150 +- 49	37.5	27	21
Ethmalosa dorsalis	235 +- 21	248 +- 71	12.5	9	9
Sardinella aurita	0 +- 0	0 +- 0	0.0	0	0
Sardinella maderensis	0 +- 0	0 +- 0	0.0	0	0
Dicentrarchus punctatus	0 +- 0	0 +- 0	0.0	0	0
Pomadasys spp.	0 +- 0	0 +- 0	0.0	0	0
Sarotherodon spp.	235 +- 34	254 +-108	4.2	3	3
Smaris melanurus	0 +- 0	0 +- 0	0.0	0	0
Cheilopogon heterurus	0 +- 0	0 +- 0	0.0	0	0
Strongylura crocodila	0 +- 0	0 +- 0	0.0	0	0
galeoides decadactylus	0 +- 0	0 +- 0	0.0	0	0
Mugil spp.	0 +- 0	0 +- 0	0.0	0	0
Liza spp.	0 +- 0	0 +- 0	0.0	0	0
Others	0 +- 0	0 +- 0	0.0	0	0
Pseudotolithus spp.	0 +- 0	0 +- 0	0.0	0	0
Caranx spp.	0 +- 0	0 +- 0	0.0	0	0
Lichia glauca	0 +- 0	0 +- 0	0.0	0	0
Other Carangidae	0 +- 0	0 +- 0	0.0	0	0

Sample size = 72
Average weight = 196
Average corrected weight= 196

Ile aux Oiseaux April-August 1979
Average length and weight of fish estimated from opercula

species	length in mm	weight in g	%	number of opercula	
				all	intact
Liza dumerili	191 +- 54	96 +- 86	9.7	3	3
Liza grandisquammis	224 +- 29	135 +- 60	38.7	12	11
Liza falcipinnis	0 +- 0	0 +- 0	0.0	0	0
Mugil curema	242 +- 0	206 +- 0	3.2	1	1
Mugil monodi	0 +- 0	0 +- 0	0.0	0	0
Mugil cephalus	0 +- 0	0 +- 0	0.0	0	0
Mugil bananensis	209 +- 27	131 +- 58	16.1	5	5
Ethmalosa dorsalis	224 +- 35	224 +- 84	22.6	7	7
Sardinella aurita	0 +- 0	0 +- 0	0.0	0	0
Sardinella maderensis	0 +- 0	0 +- 0	0.0	0	0
Dicentrarchus punctatus	0 +- 0	0 +- 0	0.0	0	0
Pomadasys spp.	0 +- 0	0 +- 0	0.0	0	0
Sarotherodon spp.	152 +- 16	74 +- 16	6.5	2	2
Smaris melanurus	0 +- 0	0 +- 0	0.0	0	0
Cheilopogon heterurus	0 +- 0	0 +- 0	0.0	0	0
Strongylura crocodila	0 +- 0	0 +- 0	3.2	1	0
galeoides decadactylus	0 +- 0	0 +- 0	0.0	0	0
Mugil spp.	0 +- 0	0 +- 0	0.0	0	0
Liza spp.	0 +- 0	0 +- 0	0.0	0	0
Others	0 +- 0	0 +- 0	0.0	0	0
Pseudotolithus spp.	0 +- 0	0 +- 0	0.0	0	0
Caranx spp.	0 +- 0	0 +- 0	0.0	0	0
Lichia glauca	0 +- 0	0 +- 0	0.0	0	0
Other Carangidae	0 +- 0	0 +- 0	0.0	0	0

Sample size = 31
Average weight = 149
Average corrected weight= 149

Ile aux Oiseaux November 1979
Average length and weight of fish estimated from opercula

species	length in mm	weight in g	%	number of opercula	
				all	intact
Liza dumerili	0 +- 0	0 +- 0	0.0	0	0
Liza grandisquammis	0 +- 0	0 +- 0	0.0	0	0
Liza falcipinnis	0 +- 0	0 +- 0	0.0	0	0
Mugil curema	220 +- 0	154 +- 0	2.5	1	1
Mugil monodi	0 +- 0	0 +- 0	0.0	0	0
Mugil cephalus	0 +- 0	0 +- 0	0.0	0	0
Mugil bananensis	221 +- 9	152 +- 22	25.0	10	8
Ethmalosa dorsalis	244 +- 27	281 +- 89	67.5	27	25
Sardinella aurita	0 +- 0	0 +- 0	0.0	0	0
Sardinella maderensis	0 +- 0	0 +- 0	0.0	0	0
Dicentrarchus punctatus	226 +- 0	136 +- 0	2.5	1	1
Pomadasys spp.	0 +- 0	0 +- 0	0.0	0	0
Sarotherodon spp.	0 +- 0	0 +- 0	0.0	0	0
Smaris melanurus	0 +- 0	0 +- 0	0.0	0	0
Cheilopogon heterurus	0 +- 0	0 +- 0	0.0	0	0
Strongylura crocodila	0 +- 0	0 +- 0	0.0	0	0
galeoides decadactylus	0 +- 0	0 +- 0	0.0	0	0
Mugil spp.	0 +- 0	0 +- 0	0.0	0	0
Liza spp.	0 +- 0	0 +- 0	0.0	0	0
Others	0 +- 0	0 +- 0	2.5	1	0
Pseudotolithus spp.	0 +- 0	0 +- 0	0.0	0	0
Caranx spp.	0 +- 0	0 +- 0	0.0	0	0
Lichia glauca	0 +- 0	0 +- 0	0.0	0	0
Other Carangidae	0 +- 0	0 +- 0	0.0	0	0

Sample size = 40
Average weight = 240
Average corrected weight= 238

Mangrove April-August 1979
Average length and weight of fish estimated from opercula

species	length in mm	weight in g	%	number of opercula	
				all	intact
Liza dumerili	0 +- 0	0 +- 0	0.0	0	0
Liza grandisquammis	215 +- 12	111 +- 23	4.4	3	3
Liza falcipinnis	0 +- 0	0 +- 0	0.0	0	0
Mugil curema	225 +- 19	170 +- 41	17.6	12	12
Mugil monodi	0 +- 0	0 +- 0	0.0	0	0
Mugil cephalus	229 +- 3	144 +- 6	4.4	3	3
Mugil bananensis	209 +- 24	131 +- 51	42.6	29	24
Ethmalosa dorsalis	219 +- 28	205 +- 73	14.7	10	10
Sardinella aurita	0 +- 0	0 +- 0	0.0	0	0
Sardinella maderensis	0 +- 0	0 +- 0	0.0	0	0
Dicentrarchus punctatus	0 +- 0	0 +- 0	0.0	0	0
Pomadasys spp.	0 +- 0	0 +- 0	0.0	0	0
Sarotherodon spp.	196 +- 19	150 +- 41	14.7	10	10
Smaris melanurus	0 +- 0	0 +- 0	0.0	0	0
Cheilopogon heterurus	0 +- 0	0 +- 0	0.0	0	0
Strongylura crocodila	0 +- 0	0 +- 0	0.0	0	0
galeoides decadactylus	0 +- 0	0 +- 0	0.0	0	0
Mugil spp.	0 +- 0	0 +- 0	0.0	0	0
Liza spp.	0 +- 0	0 +- 0	0.0	0	0
Others	0 +- 0	0 +- 0	0.0	0	0
Pseudotolithus spp.	0 +- 0	0 +- 0	0.0	0	0
Caranx spp.	0 +- 0	0 +- 0	0.0	0	0
Lichia glauca	0 +- 0	0 +- 0	0.0	0	0
Other Carangidae	0 +- 0	0 +- 0	1.5	1	0

Sample size = 68
Average weight = 151
Average corrected weight= 151

Mangrove November 1979
Average length and weight of fish estimated from opercula

species	length in mm	weight in g	%	number of opercula	
				all	intact
Liza dumerili	0 +- 0	0 +- 0	0.0	0	0
Liza grandisquammis	235 +- 0	149 +- 0	1.6	1	1
Liza falcipinnis	230 +- 36	134 +- 59	4.8	3	3
Mugil curema	214 +- 14	145 +- 28	12.9	8	8
Mugil monodi	0 +- 0	0 +- 0	1.6	1	0
Mugil cephalus	288 +- 23	302 +- 69	19.4	12	12
Mugil bananensis	219 +- 23	154 +- 66	40.3	25	24
Ethmalosa dorsalis	220 +- 41	217 +-126	6.5	4	4
Sardinella aurita	0 +- 0	0 +- 0	0.0	0	0
Sardinella maderensis	0 +- 0	0 +- 0	0.0	0	0
Dicentrarchus punctatus	0 +- 0	0 +- 0	0.0	0	0
Pomadasys spp.	0 +- 0	0 +- 0	0.0	0	0
Sarotherodon spp.	199 +- 19	155 +- 42	12.9	8	8
Smaris melanurus	0 +- 0	0 +- 0	0.0	0	0
Cheilopogon heterurus	0 +- 0	0 +- 0	0.0	0	0
Strongylura crocodila	0 +- 0	0 +- 0	0.0	0	0
galeoides decadactylus	0 +- 0	0 +- 0	0.0	0	0
Mugil spp.	0 +- 0	0 +- 0	0.0	0	0
Liza spp.	0 +- 0	0 +- 0	0.0	0	0
Others	0 +- 0	0 +- 0	0.0	0	0
Pseudotolithus spp.	0 +- 0	0 +- 0	0.0	0	0
Caranx spp.	0 +- 0	0 +- 0	0.0	0	0
Lichia glauca	0 +- 0	0 +- 0	0.0	0	0
Other Carangidae	0 +- 0	0 +- 0	0.0	0	0

Sample size = 62
Average weight = 182
Average corrected weight= 182

Coastal sand dunes

Percentage frequencies of fish species eaten by Ospreys as determined from uneaten tails.

	Feb-March n=37	April-August n=44	September-November n=56
Mugilidae	13.5	6.8	0.0
Ethmalosa dorsalis	2.7	0.0	0.0
Sardinella spp.	0.0	45.5	8.9
Dicentrarchus punctatus	0.0	2.3	0.0
Pomadasys spp.	24.2	0.0	0.0
Sarotherodon spp.	0.0	0.0	0.0
Cheilopogon heterurus	0.0	2.3	28.6
Strongylura crocodila	51.4	0.0	8.9
Galeoides decadactylus	0.0	0.0	0.0
Pseudotolithus spp.	0.0	0.0	0.0
Carangidae	0.0	36.4	50.0
Others	10.8	6.8	0.0

Mouth of the Senegal River

Percentage frequencies of fish species eaten by Ospreys as determined from uneaten tails.

	Feb-March 1979 n=52	April-August 1979 n=14	Sept-Oct 1979 n=40	Nov-Dec 1979 n=57	Dec-Jan 1980 n=60	Feb-March 1980 n=69
Mugilidae	65.4	57.1	72.5	57.9	38.3	60.9
Ethmalosa dorsalis	17.3	0.0	2.5	14.0	11.7	11.6
Sardinella spp.	0.0	0.0	2.5	0.0	0.0	0.0
Dicentrarchus punctatus	0.0	0.0	0.0	0.0	0.0	0.0
Pomadasys spp.	1.9	7.1	0.0	0.0	0.0	1.4
Sarotherodon spp.	0.0	14.3	2.5	0.0	1.7	0.0
Cheilopogon heterurus	7.7	0.0	0.0	22.8	40.0	1.4
Strongylura crocodila	0.0	7.1	0.0	0.0	6.7	18.8
Galeoides decadactylus	0.0	0.0	0.0	0.0	0.0	0.0
Pseudotolithus spp.	0.0	0.0	0.0	0.0	0.0	0.0
Carangidae	1.9	7.1	12.5	1.8	0.0	0.0
Others	1.9	7.1	7.5	3.5	1.7	1.4

Mouth of the Saloum River

Percentage frequencies of fish species eaten by Ospreys as determined from uneaten tails.

	March 1979 n=33	April-August 1979 n=17	Sept-Oct 1979 n=18	Nov-Dec 1979 n=17	Jan-May 1980 n=85
Mugilidae	24.2	64.7	33.3	70.6	37.6
Ethmalosa dorsalis	51.5	35.3	66.7	29.4	56.5
Sardinella spp.	0.0	0.0	0.0	0.0	0.0
Dicentrarchus punctatus	0.0	0.0	0.0	0.0	0.0
Pomadasys spp.	060	0.0	0.0	0.0	8.2
Sarotherodon spp.	0.0	0.0	0.0	0.0	0.0
Cheilopogon heterurus	0.0	0.0	0.0	0.0	1.2
Strongylura crocodila	0.0	0.0	0.0	0.0	2.3
Galeoides decadactylus	0.0	0.0	0.0	0.0	0.0
Pseudotolithus spp.	0.0	0.0	0.0	0.0	0.0
Carangidae	3.0	0.0	0.0	0.0	1.2
Others	15.2	0.0	0.0	0.0	4.7

Inshore islands

Percentage frequencies of fish species eaten by Ospreys as determined from uneaten tails.

	Feb-March 1979 n=46	April-August 1979 n=14
Mugilidae	50.0	42.9
Ethmalosa dorsalis	10.9	35.7
Sardinella spp.	0.0	0.0
Dicentrarchus punctatus	0.0	0.0
Pomadasys spp.	0.0	0.0
Sarotherodon spp.	15.2	0.0
Cheilopogon heterurus	0.0	0.0
Strongylura crocodila	13.0	14.3
Galeoides decadactylus	0.0	0.0
Pseudotolithus spp.	0.0	0.0
Carangidae	0.0	0.0
Others	13.0	7.1

Shallow coastal tidewaters (Djas pond south and north combined)
Percentage frequencies of fish species eaten by Ospreys as determined from uneaten tails.

	02/01 1979 n=218	03/01-02/02 1979 n=213
Mugilidae	52.3	35.2
Ethmalosa dorsalis	11.4	34.7
Sardinella spp.	6.9	0.5
Dicentrarchus punctatus	0.5	0.5
Pomadasys spp.	0.9	1.4
Sarotherodon spp.	0.0	0.0
Cheilopogon heterurus	23.4	26.8
Strongylura crocodila	0.5	0.0
Galeoides decadactylus	0.0	0.0
Pseudotolithus spp.	0.0	0.0
Carangidae	0.9	0.9
Others	0.0	0.0

Shallow coastal tidewaters (Djas pond south only)
Percentage frequencies of fish species eaten bu Ospreys as determined from uneaten tails.

	28/12 1977	29/12-18/01 1978	19/01-13/03 1978	03/02-14/02 1979	15/02-28/02 1979	01/03-12/03 1979	13/03-23/03 1979
	n=72	n=148	n=238	n=57	n=88	n=69	n=69
Mugilidae	33.3	20.9	18.4	49.1	36.4	50.7	44.9
Ethmalosa dorsalis	8.3	5.4	11.3	26.3	39.8	44.9	37.7
Sardinella spp.	0.0	0.7	0.0	0.0	0.0	0.0	1.4
Dicentrarchus punctatus	1.4	9.5	6.7	0.0	1.1	2.9	0.0
Pomadasys spp.	1.4	1.4	2.5	3.5	1.1	2.9	4.3
Sarotherodon spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cheilopogon heterurus	36.1	40.5	49.2	15.8	15.9	4.3	4.3
Strongylura crocodila	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Galeoides decadactylus	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pseudotolithus spp.	0.0	0.0	0.0	0.0	0.0	0.0	2.9
Carangidae	5.6	2.7	2.1	5.3	5.7	0.0	1.4
Others	14.0	18.2	9.7	0.0	0.0	1.4	2.9

Shallow coastal tidewaters (Djas pond south only)
Percentage frequencies of fish species eaten by Ospreys as determined from uneaten tails.

	24/03-16/04 1979 n=63	17/05-20/05 1979 n=86	21/05-August 1979 n=27	31/08-24/10 1979 n=29	25/10-15/11 1979 n=13	16/11-23/12 1979 n=43
Mugilidae	33.3	2.3	18.5	79.3	53.8	32.6
Ethmalosa dorsalis	54.0	93.0	77.8	13.7	23.1	53.5
Sardinella spp.	0.0	0.0	0.0	0.0	0.0	4.7
Dicentrarchus punctatus	3.2	0.0	0.0	0.0	1.5	0.0
Pomadasys spp.	4.8	1.2	0.0	3.4	0.0	0.0
Sarotherodon spp.	1.6	0.0	0.0	0.0	0.0	0.0
Cheilopogon heterurus	0.0	0.0	0.0	0.0	0.0	2.3
Strongylura crocodila	0.0	0.0	0.0	3.4	0.8	2.3
Galeoides decadactylus	0.0	0.0	0.0	0.0	0.0	0.0
Pseudotolithus spp.	0.0	0.0	0.0	0.0	0.0	0.0
Carangidae	0.0	0.0	3.7	0.0	0.0	2.3
Others	3.2	2.3	0.0	0.0	0.0	0.0

Shallow coastal tidewaters (Djas pond north only)
Percentage frequencies of fish species eaten by Ospreys as determined from uneaten tails.

	02/02-14/02 1979 n=56	15/02-28/02 1979 n=36	01/03-09/03 1979 n=35	10/03-23/03 1979 n=63
Mugilidae	58.9	47.2	74.3	60.3
Ethmalosa dorsalis	28.6	38.9	22.9	27.0
Sardinella spp.	0.0	0.0	0.0	0.0
Dicentrarchus punctatus	0.0	2.8	0.0	0.0
Pomadasys spp.	1.8	0.0	0.0	3.2
Sarotherodon spp.	0.0	0.0	0.0	0.0
Cheilopogon heterurus	3.6	5.6	2.9	3.2
Strongylura crocodila	0.0	0.0	0.0	0.0
Galeoides decadactylus	0.0	0.0	0.0	0.0
Pseudotolithus spp.	0.0	0.0	0.0	0.0
Carangidae	0.0	2.8	0.0	3.2
Others	7.1	2.8	0.0	3.2

Shallow coastal tidewaters (Djas pond north only)
Percentage frequencies of fish species eaten by Ospreys as determined from uneaten tails.

	24/03-14/04 1979 n=36	15/04-August 1979 n=20	30/08-30/10 1979 n=35	31/10-15/11 1979 n=14	16/11-21/12 1979 n=53	22/12-15/05 1980 n=82
Mugilidae	38.9	30.0	91.4	78.6	43.4	48.8
Ethmalosa dorsalis	44.4	60.0	8.6	7.1	28.3	24.4
Sardinella spp.	0.0	0.0	0.0	0.0	0.0	0.0
Dicentrarchus punctatus	2.8	0.0	0.0	7.1	0.0	3.7
Pomadasys spp.	2.8	0.0	0.0	0.0	1.9	6.1
Sarotherodon spp.	0.0	0.0	0.0	0.0	0.0	0.0
Cheilopogon heterurus	2.8	0.0	0.0	0.0	0.0	8.5
Strongylura crocodila	2.8	0.0	0.0	7.1	24.5	2.4
Galeoides decadactylus	0.0	0.0	0.0	0.0	0.0	0.0
Pseudotolithus spp.	2.8	0.0	0.0	0.0	0.0	0.0
Carangidae	2.8	0.0	0.0	0.0	1.9	0.0
Others	0.0	10.0	0.0	0.0	0.0	6.1

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